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HYDROBIOLOGY OF THE ALVISO SALT PONDS

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INTRODUCTION

The Alviso ponds of the Leslie Salt Company border San Francisco Bay, California, where former salt marsh has been reclaimed for salt production by solar evaporation of sea water. Organisms enter the artificial ponds by natural means of dispersal; since plants and animals do not interfere with salt production, nothing is done to curb their growth. The organisms able to tolerate the environment are present in such numbers that algae and chromogenic bacteria color the water, and arthropods are conspicuous.

In the techniques associated with salt production (Tressler and Lemon 1951), ponds are used in series with increased salinity in successive ponds. Studies such as that of Ferroniére (1901) on similar ponds in France showed that as the salt content increases the number of animal species decreases due to selection of types able to withstand the increasingly difficult environment. The presence of dense populations of relatively few species would seem to make the ponds favorable for study of the interaction of a salt water environment and the organisms in it. However, although certain ecological aspects of ponds of high salinity have been reported by Peirce (1914) and Baas-Becking (1925), California salt ponds of relatively low salt content do not seem to have been subjected to intensive study, especially with reference to the physical and chemical factors. The first six ponds of the Alviso Plant were selected for investigation. They provide a specialized marine habitat in which the salinity ranges from brackish bay water (pond 1) to about four times that of ocean water (pond 6).

The distribution of organisms within the ponds and the environmental factors presumably influencing their distribution were investigated by routine sampling at approximately weekly intervals during 1951 and less frequently during 1952. The same general trends were observed during the second year. With the few exceptions noted, the data presented were obtained in 1951.

The Alviso ponds (Figs. 1 and 2) lie between the estuaries (sloughs) of intermittent streams and are, therefore, of irregular size and shape. Levees protect them from tides and from land drainage. Areas of individual ponds are: No. 1—310 acres; 2—960; 3—1190; 4—280; 5—900; 6—600. Water from the Bay can be taken into pond 1 at high tide over a flood gate across Charleston Slough. When evaporation in the ponds lowers their surface levels, water flows by gravity through ponds 1, 2, and 3 via siphons and canals between them. Pond 4 is now by-passed, and since it is not used in the series, it is ignored in the following discussion. Water is pumped from pond 3 into 5, from which it flows into pond 6. Since each pond is supplied with water from the one preceding it, there is increased salinity in each pond of the series.

ACKNOWLEDGMENTS

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PHYSICAL AND CHEMICAL FACTORS

Rainfall

Method.—Rainfall data were obtained from the Naval Air Station, Moffett Field, California, which borders the ponds.

Results.—During a fourteen year period for which records are available, the average (normal)

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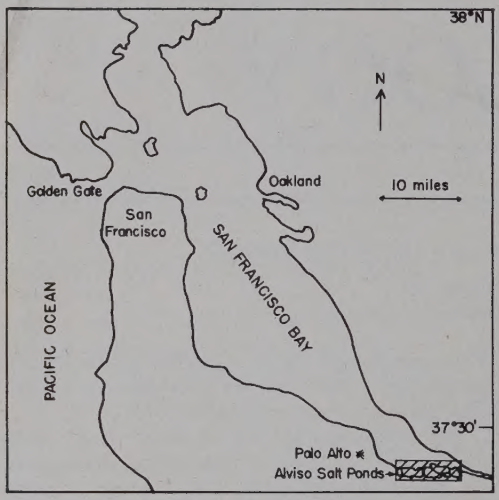


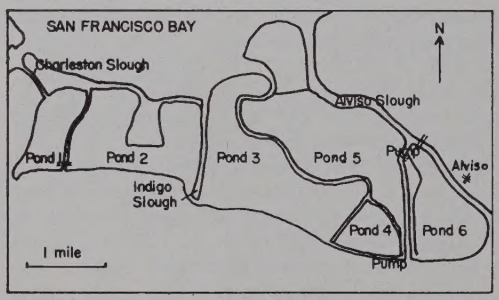


FIG. 1. Southern San Francisco Bay.
FIG. 2. Ponds 1-6, Alviso plant, Leslie Salt Company.

rainfall was 10.24 inches (26 cm.) per year. Figure 3 shows mean monthly and normal rainfall during the years the study was made.

Discussion.—The Alviso ponds, protected from coastal climatic conditions by a mountain range, lie in a region that has a large number of days with full sunshine during a rainless period from May to October. (Peirce 1914, discusses the climate in relation to salt production.) Rains dilute the ponds during winter and spring, making it possible for certain organisms to live in ponds from which they may be excluded by the higher salinity present during summer and fall.

The time at which rains fall is significant because storms late in the season can retard activity of algae in the ponds. Rainfall during 1950-1951 was above normal so that the ponds were diluted more than usual. However, since most of the rain fell in late autumn and early winter, weather conditions allowed the bloom of algae to start in late January, as early as in a normal year. In contrast, during 1951-1952 rains continued into late spring. Cloudiness and colder weather during the storms delayed the start of phytoplankton growth. Because of the shorter growing season, the crop of algae in 1952 was much reduced compared to that in 1951.

Temperature

Method.—The ponds are so shallow (average depth of ½ meter) that water temperatures were taken only at the surface with a laboratory-type stem thermometer, read to the nearest 0.5°C. Data were obtained at weekly intervals.

Results.—Mean monthly air and water temperatures are shown in Figure 4. Annual mean water temperatures were 16.3°C., 19.5°C., and 21.8°C., at 9 A.M., 12 M., and 3 P.M., respectively. The extreme range during the year was 25°C.—from 8° in January to 33° in August. Beginning in April and continuing through September, the mean water temperature exceeded that of the air.

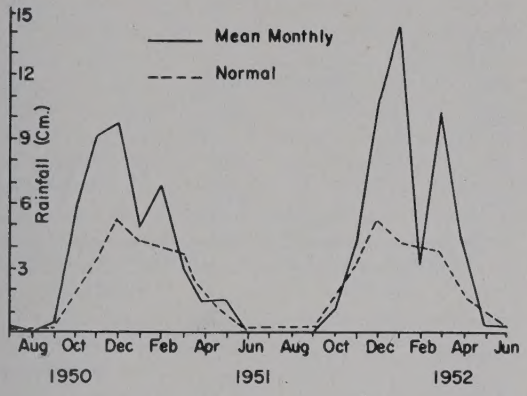
Pond temperatures are very sensitive, especially in spring, to changes in the weather. Noon temperatures in April (Table I), illustrates what changes are possible in a one week period. The weather from April 2 to 10 was clear; the water warmed to summer temperature. Then a week of cloudy weather caused an eleven degree drop in temperature. Lack of smoothness of the curve of Figure 4 is due to fluctuations of this sort, as well as to incompleteness of data.

TABLE I. Water and air temperatures, April, 1951

	Water Temperature	Air Temperature
April 2.....	19.0° C.	17° C.
9.....	24.5	23
10.....	27.5	24
17.....	16.5	16

There were great diurnal temperature fluctuations during the warmer part of the year because the ponds lack deep water in which surface temperature changes may be dissipated. The diurnal range varied from as little at 3.5°C. in January to as much as 12° in August. During the warmest part of the year, water temperatures may rise at the rate of more than one degree per hour during the morning and reach a peak at 1 or 2 P.M.

Discussion.—Summer et al. (1914) reported the mean annual temperature of San Francisco Bay to be 12.9°C. The annual mean of the ponds is 21.8°C. in mid-afternoon. Although winter temperatures in the ponds may be as low as in the Bay, summer temperatures are much higher. Organisms recruited to the ponds from the Bay



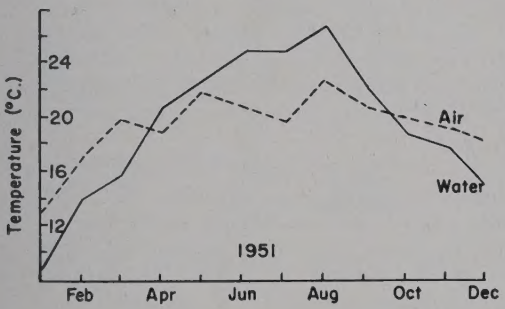


FIG. 3. Mean monthly and normal rainfall, Moffett Field, Calif.

FIG. 4. Mean monthly air and water temperatures.

are subjected to higher mean and higher maximum temperatures, and to greater annual and diurnal ranges of temperature.

Salinity

Method.—Salinity, which is defined as total salts in grams per kilogram, is abbreviated to o/oo (parts per 1000) in the following discussion. It was derived from chlorinity, determined by titration of halides with silver nitrate, using the standard conversion factor of (roughly) 1.805 X Cl o/oo = S o/oo (Sverdrup et al., 1942). Determination of salinity from chlorinity would be ruled out if there were a change in ionic proportions due either to dilution by fresh water or to precipitation of salts. The Bay water that enters the ponds is diluted in winter: the salinity of Charleston Slough may fall to as low as 14 o/oo, recorded in February. However, water is not admitted until May when the salinity is above 20 o/oo. During 1951 the water entering the ponds range from 23 o/oo in May to a high of 30 o/oo in September.

Analyses have shown only minor changes in the ratio of ions in the intake water. With the exception of carbonate, and with it some calcium, ionic proportions present in ocean water are maintained in the ponds up to a salinity of 170 o/oo, when gypsum precipitates. Gypsum approaches saturation at the highest salinity (153 o/oo) attained in pond 6, but it does not visibly precipitate. It would seem therefore that determination of total salts in the Alviso ponds by titration of halides with silver nitrate should be feasible in the range of salt concentrations concerned.

Results.—Figure 5 shows mean monthly salinities at selected stations in the five Alviso ponds. During winter and spring the water in each pond tends to become homogeneous. After flow of water begins in May, a gradient of salt concentration becomes established from inlet to outlet of each pond. Decline in salinity during June and July in the first three ponds was the result of dilution by water of lower salinity immediately after flow of water began. Salt concentrations then rose to a high in September, after which the ponds were diluted again by rains.

The mean annual salinity ranged from 27.4 o/oo at the inlet of pond 1 to 111 o/oo at the outlet of 6. The average mean annual salinity for each of the five ponds, computed by averaging salinities from all stations within a pond, is shown in Table II, together with the annual maximum and minimum and the annual range of salinity.

TABLE II. Salinity, Alviso Ponds 1-6

Pond	Average Mean Annual Salinity	Max. and Min. Salinity	Annual Range of Salinity
1	27.5 o/oo	23 - 32 o/oo	9 o/oo
2	33	27 - 38	11
3	45	40 - 53	13
5	63.5	50 - 86	36
6	94	61 - 153	92

Discussion.—Pond 1 is always brackish; pond 2 fluctuates to both sides of oceanic salinity; ponds 3-6 are always more saline than the ocean. Table II shows the range of salinity to increase in successive ponds during the year. The increasing range of salinity which must be tolerated by organisms living in a pond throughout the year, as well as the increase in salinity itself, seems to be a factor making the later ponds a more difficult environment.

Hydrogen Ion Concentration

Method.—The concentration of hydrogen ion was determined in the field with a portable Beckman Model G pH meter, equipped with an electrode designed for use in alkaline solutions.

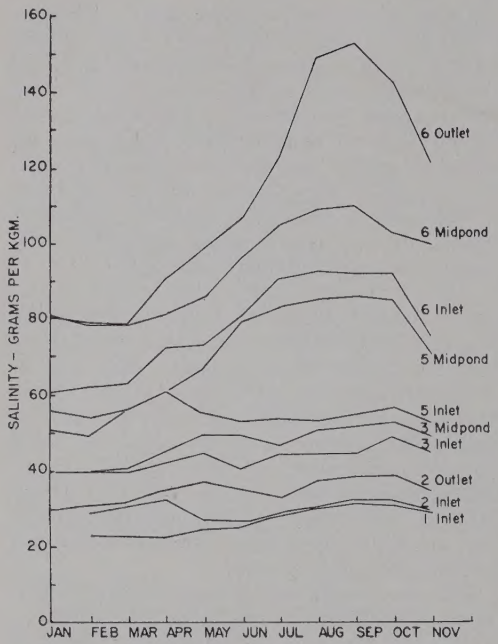


FIG. 5. Mean monthly salinity at stations indicated.

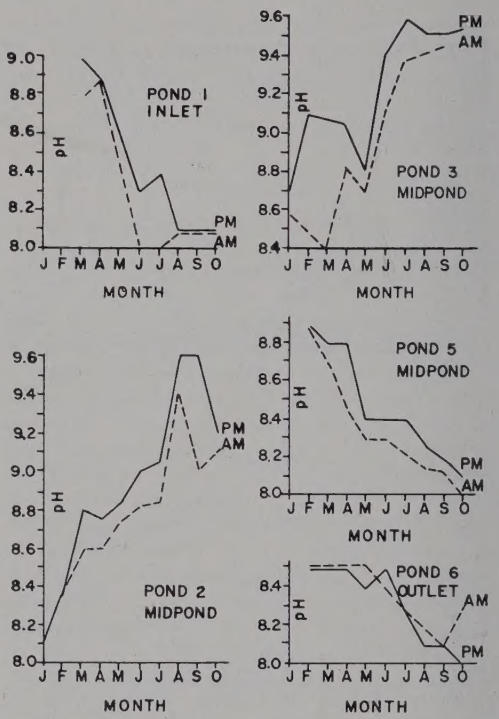


FIG. 6. Mean monthly ph values.

Results.—The pH in Charleston Slough averaged 7.8 during the period when water from it entered pond 1. Higher values occurred in spring when the slough water had a mean pH of 8.15. The first three of the Alviso ponds are more alkaline than the bay water that enters them. At the inlet of pond 1 (Fig. 6.) the annual mean pH was 8.35, with highest values occurring in spring before entry of water from the bay. In contrast, highest pH occurred in summer in pond 2 and 3. In pond 2 the annual mean for the entire pond was 8.8; at the mid-pond station the afternoon averages were 9.0 for the entire year, and 9.6 during August and September. In pond 3 the annual mean at mid-pond was 8.9 in the morning, 9.2 in the afternoon, and from June to October the mean in the afternoon was 9.5.

In the more saline water of ponds 5 and 6 pH values were below those of previous ponds, and the seasonal trend was downward from a high in spring. The annual mean pH was 8.4 in pond 5 and 8.3 in pond 6. At the outlet of pond 6, where highest salinities occur, the average pH was 8.1 during August and September.

The diurnal range of pH was usually 0.2 to 0.4 of a unit. For example, in midsummer, the time of highest pH in ponds 2 and 3, the pH at dawn on July 30 was 8.75 in pond 2 (then with a salinity of 34 o/oo), and 9.4 in pond 3 (then with a salinity of 49 o/oo). By mid-afternoon the pH had risen to 9.1 in pond 2 and to 9.8 in pond 3.

Discussion.—The pH of sea water depends largely on the ratio of CO_3^{--} to HCO_3^-. The relatively minor diurnal increase in pH in the Alviso ponds is probably due to algal assimilation of CO_2 and HCO_3^-, which increases the proportion of CO_3^{--}. The larger seasonal changes in pH, and the much higher pH relative to the oceans, seem to result from increasing salinity which brings about supersaturation of $CaCO_3$, even beyond the apparent supersaturation present at oceanic salinity (see Buch et al., 1932; Wattenberg and Timmermann 1936). Until carbonate is lost by precipitation, there is increase in pH. In ponds 2 and 3 $CaCO_3$ does not precipitate; when high pH values are attained in summer, they are maintained day and night, presumably due to the large reservoir of inactive CO_3^{--}, which buffers any decrease in pH due to CO_2 from respiration or from the atmosphere. The high pH in summer may be above the tolerance of those marine animals (especially larvae) which are adapted only to the lower and more constant pH of the oceans. The high pH may also be limiting, not only to plant distribution within the ponds, but to plant productivity

as well, because of the limitation of carbon source for photosynthesis. At pH 9 the concentration of CO_2 is practically zero, and HCO_3^- is less abundant than CO_3^{--} (Mobert et al., 1934). Algae unable to utilize HCO_3^- (Österlind 1950) might not photosynthesize in the alkaline ponds. Plants able to assimilate HCO_3^- might continue to live, but in the range between pH 9.5 and 10.0 not only does the concentration of HCO_3^- become so low that carbon availability may limit plant growth, but the concentration of hydroxyl ion may become toxic.

At a salinity of about 80 o/oo, $CaCO_3$ precipitates. This happens in ponds 5 and 6, where the removal of CO_3^{--} is indicated by the decrease in pH. At the outlet of the last of the Alviso ponds (pond 6), gypsum ($CaSO_4 \cdot 2H_2O$) reaches saturation at the salinity attained in August. (In the pond subsequent to 6 gypsum comes out of solution visibly, and the environment becomes so altered that there is a sharp change in the flora.)

Dissolved Oxygen

Method.—Dissolved oxygen was determined by the unmodified Winkler method. The technique and its modifications for use in sea water are reviewed by Jacobsen et al. (1950).

Results.—Figure 7 illustrates the mean monthly concentrations of dissolved oxygen found at selected stations within the ponds. In addition to seasonal changes, differences in morning and evening values and relation to the calculated concentration at saturation are included. Data for pond 1, being similar to those of pond 2, are not shown. Two stations are shown for pond 2 because at shore (Fig. 7B) decomposition of macroscopic algae during summer and fall creates a limited area with lower concentrations of oxygen than in the main body of the pond (Fig. 7A).

In Table III mean annual oxygen concentrations indicate two trends: a decrease in concentration of dissolved oxygen with increase in salinity, and a diurnal increase from sub-saturation in the morning to super-saturation in the afternoon. Because there are greater diurnal changes than the mean concentrations (shown in Table III and Figure 7) indicate, an example of a large diurnal range of dissolved oxygen as shown in Table IV.

Discussion.—The amount of oxygen that can be dissolved in water varies inversely with both temperature and salinity. Both factors are variable in the Alviso ponds. The temperature range concerned is approximately from 10° to 30°C. At 30° water of ocean salinity is saturated with 4.5 ml of O_2 per liter, and at 10°C. with 6.4 ml/l (Fox 1907). Because of their low salinity, the

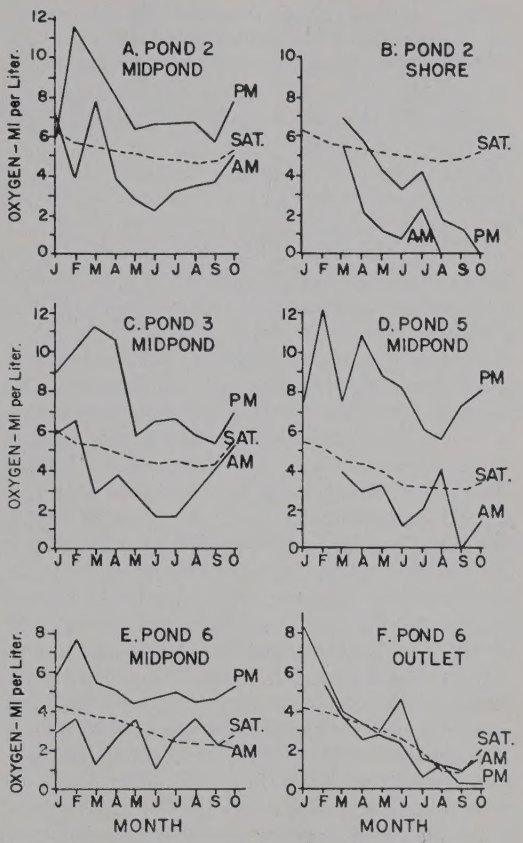


FIG. 7. Mean monthly dissolved oxygen concentrations.

TABLE III. Mean annual oxygen concentrations

Midpond Station:	Mean O_2 Conc. (ml/l) AM	PM	Calculated* Conc. at Saturation (ml/l) AM	PM	Calculated Percent of Saturation (ml/l) AM	PM	Mean Salinity (o/oo)
Pond 2....	4.4	7.5	6.0	5.5	73	137	33.6
3....	3.8	7.5	5.3	4.8	71	155	47.0
5....	2.3	6.8	4.5	4.3	51	157	70.5
6....	2.6	5.2	3.5	3.2	74	163	93.5

*Saturation calculated at mean salinity for mean temperature of 16.3° C. for morning and 21.8° C. for afternoon.
Insufficient data for inclusion of pond 1.

first two of the Alviso ponds can dissolve as much, or more, oxygen than ocean water, but later ponds cannot. Table III illustrates the downward trend of oxygen concentration with increase in salinity in the ponds. Diurnal differences in concentration are due to biological activity: respiratory consumption depletes oxygen at night, when there is no compensatory production of oxygen by algae, but during the day the water becomes supersatu-

TABLE IV. Diurnal changes in dissolved O_2, temperature, and pH, Alviso Pond, 3, July 2, 1951

Time	Water Temp. (° C.)	pH	Dissolved Oxygen (ml/l)	Calculated Conc. of O^2 at Satur. (ml/l)	Calculated* Percent of Saturation
0630	19.5	9.25	0.77	4.9	15
1100	22.5	9.6	6.2	4.8	129
1500	23.5	9.6	5.6	4.7	119

*Percent saturation at temperature indicated and Salinity of 45 o/oo.

rated because the oxygen evolved by photosynthesis is not lost to the atmosphere as rapidly as it is produced.

In most of the area of the salt ponds the water is well aerated during the day, but organisms dependent on dissolved oxygen must be able to tolerate, at least for short periods, the low concentrations that occur at night. There are limited areas of the first two ponds in which very low oxygen concentrations occur not just at night, but during the day as well, both in summer and fall. These anoxic areas result from bacterial activity during putrefaction of accumulations of green algae in a zone about 100 meters wide along the shore. The water adjacent is well-aerated and supports a good growth of green algae and associated animals (see below). During a cycle of sulfur bacteria, whose ecology has been discussed by Bavendamm (1924), hydrogen sulfide and colloidal sulfur are liberated.

At the shore of pond 2 (Fig. 7B) putrefaction of the alga *Rhizoclonium* reduced the concentration of dissolved oxygen in June. The region became anoxic in August when a greater quantity of the alga *Enteromorpha* putrefied in the same area. The anoxic condition continued into winter. From February until the start of the next cycle (in June) the region was as well-aerated as the rest of the pond. The enriched black mud was then available to aerobic bottom-feeding animals.

Nitrogen and Phosphorus

Methods.—Phosphate was determined by the molybdate method (Wooster and Rakestraw 1951); nitrate by di-phenylbenzidine (Atkins 1932); ammonia by direct Nesslerization by the Witting-Buch technique (Wirth and Robinson, 1933).

Results.—Data are summarized in Table V to show concentrations of nutrients during the two distinctive periods: prior to and subsequent to intake of water from the bay. Prior to water intake (data shown for March) nitrate was abundant in all ponds, decreasing in concentration from highest in pond 1 to lowest in pond 6. Phosphate was also high in concentration in all ponds except 1, and increased through the series to a high in pond 6. During the period of water intake and flow through the series, nitrate, although present in the Slough, was very low in concentration in all ponds. Phosphate was abundant in the Slough and in pond 1 but, with the exception of the shore of 2, there were low concentrations of phosphate in ponds 2 and 3. Phosphate was present in high concentrations again in ponds 5 and 6. Ammonia was not determined prior to flow of water. From May to October the concentration of ammonia was high in the Slough, relatively low in ponds 1 and 2 (again with the exception of the shore of 2) and then higher again in ponds 3, 5, and 6.

TABLE V. Concentrations of nutrient salts in μg-A/1, Charleston Slough and Alviso Ponds 1-6

Location	Mean Conc., March*		Mean Conc., May to October**		
	NO_3-N	PO_4-P	NO_3-N	PO_4-P	NH_4-N
Slough	28.5	1.5	12.0	8.0	34.0
Pond 1	32.5	0.5	0.7	6.0	8.0
Midpond 2	25.0	2.1	0.5	0.6	12.0
Shore 2	...	...	0.7	3.0	22.5
Pond 3	19.6	2.1	1.3	0.3	17.5
Pond 5	14.0	4.8	1.5	13.0	24.0
Pond 6	12.5	7.5	1.7	13.0	17.0

*Period prior to intake of bay water.
**Period of water intake.

Discussion.—Because they are operated in series, each of the ponds depends on the water from the one preceding it for replenishment of its supply of nutrient salts. Plant nutrients entering from the bay are subject to use and re-use in cycles of assimilation by algae and re-mineralization by bacteria. By analogy with ocean conditions (Waksman et al., 1933) it is not unexpected that during much of the year ammonia is the principal form of available nitrogen in the shallow Alviso ponds. Only during winter, when algal activity is low, is there time for bacterial conversion of ammonia to nitrate. The higher concentrations of ammonia and of ingoranic phosphate at "shore 2" in Table V is probably indicative of their release from decaying algae during summer and fall.

The apparently higher concentrations of nutrients, especially of phosphate, in ponds 5 and 6 may have been the result of decomposition of animals that died after entry from pond 3, but more probably were a result of the evaporation of water. As the total salt content increased, the concentration of nutrient salts increased with the rest. However, unlike the other salts, the increase in concentration of nutrients was delayed while they were incorporated into plants and animals.

Minor Elements (Micronutrients)

Method. In order to determine whether some minor-element requirement might be limiting to algal growth in the ponds, samples were sent to a commercial analytical laboratory for semi-quantitative spectroscopic analyses.

Results. In ponds 1 and 2 the concentrations of iron and boron were ½ those present in the water that enters the Alviso series. Si, Al Cu, and Cr in the ponds remained at about the same relative concentrations as in the water of the Bay. Ni, Mn, V, and Co, were too low in concentration to be detectable, by the technique used, in the intake water and within the Alviso ponds.

Discussion. The iron lost from solution in the first two ponds is probably associated with the phosphate that remains in the black mud after decomposition of large algae (Hayes and Coffin 1951). Although the amount of iron that remained in solution should be adequate for algal requirements, there may have been sub-minimal concentrations of Mn or Co.

Organisms of the Alviso Salt Ponds

In general only the more numerous plants and animals are considered in the following non-quantitative account of the organisms of the Alviso ponds. At approximately weekly intervals phytoplankton samples were collected in bottles, and zooplankton was taken with a tow net of nine inch diameter, #12 bolting cloth, 125 meshes per inch. Larger plants and animals were taken by hand or by dip net.

Plants

With the exception of one higher plant and excluding bacteria, the plant life of the ponds consists entirely of algae. Green algae (Chlorophyta) are the most important.

A. Cyanophyta. Blue-green algae are abundant in the Alviso ponds only where decomposition of green algae provide a substrate comparable to soft organic mud which, according to Schuster (1952), favors the growth of blue-green algae. Cyanophyta observed were principally species of *Oscillatoria,* but species of *Anabaena* and *Nostoc* were *also* observed.

B. Chrysophyta. Two diatoms are conspicuous in the water that enters the ponds. *Melosira moniliformis* (Müller) Agardh, and *Pleurosigma elongatum* W. Smith, were present in practically all plankton collections from the first pond and the inlet of the second. With the exception of *Melosira,* the diatoms of the ponds are all Pennales, characteristically littoral forms whose natural history has been described by Nelson (1947). *Pleurosigma* is the most numerous of the pennate diatoms in the Slough and in the first pond, but it does not thrive in later ponds. Several diatoms associated with the decomposing green algae include *Achnanthes longipes* Agardh, *Grammatophora marina* (Lyngbye) Kützing, *Campylosira* sp., *Thalassionema nitzschoides* Grunow, *Navicula* sp., *Nitzschia closterium* (Ehrenberg) W. Smith, and *Nitzschia longissima* (Brebisson) Ralfs. One large naviculoid, apparently more free-swimming than the rest of the pennate diatoms of the ponds, is probably *Amphiprora gigantea* var. *sulcata* (O'Meara) Cleve. Diatoms seem limited to the first two of the Alviso ponds, and to the inlet of the third. With the exception of *Amphiprora,* which has been found at a salinity of 50 o/oo, diatoms seem limited to salinities below 40 o/oo in the Alviso ponds.

C. Chlorophyta. *Dunaliella salina* (Dunal) Teodoresco, one of the Volvocales, was present for a brief period in the fifth pond in early April. This is noteworthy since the salinity was not extremely high at the time, and yet *Dunaliella* is the most conspicuous alga in brines of really high salinity, subsequent to precipitation of gypsum, where it and *Stephanoptera gracilis* (Atari) G. M. Smith become the dominant algae in water up to saturation with sodium chloride.

In the brackish water of the first two ponds the principal plants during summer and fall are macroscopic green algae. Of these, *Bryopsis hypnoides* Lamaroux, one of the Siphonales, is of minor concern because it grows only in a few clumps on the bottom and on pilings near the inlets of ponds 1 and 2. The most prevalent algae are *Rhizoclonium* sp. (probably *R. implexum* (Dillwyn) Kützing), one of the Cladophorales, and *Enteromorpha* sp. (probably *E. intestinalis* (L.) Link), one of the Ulvales. These two algae, which are characteristic of brackish water, are present from June or July on throughout summer and fall. *Rhizoclonium* may appear first, but is followed very shortly by *Enteromorpha,* which grows anchored to the bottom with *Rhizoclonium* intertwined among its filaments. Portions of this bottom growth become detached after the first warm days of summer, and floating masses of the algae appeared (at the end of July, 1951) on the pond surface. Here they began to undergo bacterial decomposition, which was completed wherever the masses are driven. Winds and currents carry them to the south shores and to the outlets of the first two ponds. They form conspicuous zones where decomposition takes place.

Enteromorpha and *Rhizoclonium* disappeared in early winter. In late winter a single-celled

green alga, *Stichococcus bacilaris* Nägeli, one of the Ulotricales, bloomed in ponds 1 and 2. The bloom declined in May when water was first admitted from the bay. By July or August *Stichococcus* had disappeared and been replaced by the macroscopic algae. *Rhizoclonium* and *Enteromorpha* do not extend into the Alviso series beyond pond 2. They are apparently unable to tolerate the higher salinity in ponds 3 to 6 in which *Stichococcus* is the principal plant throughout the year.

D. Pyrrophyta. Dinoflagellates are not numerous in the Alviso ponds. *Oxyrrhis marina* Dujardin, reported by Kirby (1932) to be the most common flagellate in California salt marshes, was the most frequently found.

E. Angiospermae. The only higher plant in the Alviso ponds is "ditch grass," *Ruppia maritima* Linnaeus, which appeared in the second pond early in August, when the salinity was 28.2 o/oo. *Ruppia* did not establish itself elsewhere in the ponds and due to its limited growth is of uncertain importance to their economy. *Zostera,* which is typical of bays and estuaries, was not observed in the Alviso ponds.

Animals

A. Protozoa. Only incidental observations were made of protozoa. *Euplotes* spp. were the most common ciliates of the first two ponds, being always present among the large green algae. In ponds of higher salinity, a free-swimming *Condylostoma* (probably *C. patens* (Müller) Dujardin), and *Fabrea salina* Henneguy were the most numerous. Also observed were species of *Didinium, Coleps, Lionotus, Trachelocera,* unidentified tintinnids, and *Vorticella*-like colonies.

B. Coelenterata. *Tubularia crocea* Agassiz grows on the flood gate at Charleston Slough, but occurs nowhere else in the ponds. One species of small anemone, probably *Diadumene luciae* (Verrill) is present on pilings and floating logs in the first two ponds. Coelenterate planulae, presumably of the above species, were taken in late June as far into the series as the inlet of the third pond. Adults were not observed except in the first pond and at the inlet of the second.

C. Nemathelminthes. No attempt was made to identify the nematodes which are prevalent among the decaying organic matter and in the black mud of the ponds.

D. Nemertinea. *Tubulanus sexlineatus* (Griffin) is commonly found among decomposing algae, especially among *Bryopsis* in pond 1. This nemertean is apparently a predator on the polychaete worm living in the matrix of decomposing algae.

E. Annelida. The most prevalent worm in the Alviso ponds is the polychaete *Polydora ligni* Webster. Adults live on the bottom in loose tubes constructed of dead algae. Planktonic larvae were first noted in March. During April and May, larvae from the 3-segmented to the 18-segmented stage were numerous. Numbers decreased during the latter part of May, and none was taken later than June. During this period the range of salinity was from 23 o/oo in the first pond to about 40 o/oo in the inlet of the third, which is the farthest that *Polydora* extends into the series of ponds. The egg apparently hatches in the 3-segmented stage. After 2-3 weeks of plankton feeding, the larvae reach the 15-18 segmented stage at which they settle to take up the adult tube-dwelling habit.

Polydora is the only bottom-dwelling invertebrate with a planktonic larva which is present in sufficient numbers to be of significance to the ecology of the ponds. During the spring bloom of *Stichococcus,* which coincides with the peak of spawning of *Polydora,* the planktonic worm larvae exceed in number all other plankton-feeding organisms in the first two ponds. The larval worms are eaten by fish that develop simultaneously in the same ponds. As evidenced by the relatively few adult worms, there is a great loss in number during the larval free-swimming period.

F. Trochelminthes. On species of rotifer, probably *Brachionus plicatilis* Müller, appeared at times in plankton collections from the second and third ponds, but was most numerous at the inlet of pond 5 during spring when the salinity was 56-62 o/oo. At this station in spring there is a complex succession of alternating and fluctuating populations of *Stichococcus,* of algal-feeding protozoans, *Fabrea* and *Condylostoma,* as well as of the rotifer.

G. Arthropoda. In numbers of individuals the animal life of the Alviso ponds is predominantly of Arthropods. Detritus-feeding insects are present in all the ponds, and filter-feeding crustacea include copepods in earlier ponds, and a branchiopod, *Artemia,* in later ponds.

(1) Branchipoda. *Artemia salina* Linnaeus is the predominant animal in the sixth pond. Because of its tolerance to high salt concentrations, *Artemia* has been of physiological interest. It is reported to maintain the salt content of its body fluids always below that of its medium (Medwedewa, 1927; Kuenen, 1939) and that, therefore, it may be salt deficient at low salinities; the optimum salinity for *Artemia* is in the range from 2X to 5X sea water, which is a salinity range from 70 o/oo to 175 o/oo. The salinity of

pond 6 ranges from 61 o/oo to 153 o/oo during the year. It may thus be that osmotic relations rather than fish predation (Whitaker 1940) may limit *Artemeia* to high salinities. The life history and stages of development of *Artemia* are well known (Heath 1924). Under optimal laboratory conditions sexual maturity is said to be reached in three weeks. Under natural conditions in the Alviso ponds, maturity was reached in about four weeks during the period when water temperatures exceeded 20°C., but during spring and late fall development was slower. There were an estimated eight generations per year. During summer and fall there is a steady production of eggs which hatch immediately on being laid. There are also winter eggs whose delayed hatching seems favored by alternate drying and submersion. The largest population of *Artemia* observed in the Alviso ponds weighed 13 gms per cubic meter (dry weight). With an estimated eight generations per year, the production of *Artemia* in pond 6 amounted to about 56 lbs. per acre per year.

(2) Copepoda. Three of the eleven species of free-swimming copepods reported by Esterley (1924) from San Francisco Bay were collected in the Alviso ponds, and a fourth species, reported by Johnson (1939) from southern California estuaries and salt ponds, has also been identified. The most prevalent copepod in the Slough and in the first pond is *Acartia tonsa* Dana, which also appeared in winter collections (February and March) in ponds 2 and 3. During summer it was numerous in the tidal current entering pond 1. A related species, *Acartia clausi* Giesbrecht, occurred in pond 3 in winter when *Eurytemora hirundoides* Nordquist was also present. *Pseudodiaptomus euryhalinus* Johnson, which is the most salt-tolerant copepod in the Alviso ponds, thrived in pond 3 during summer. It entered pond 5 with water from pond 3, but it was taken only once beyond the inlet: at mid-pond when the salinity was less than 60 o/oo. Johnson (1939) reports finding it at salinities from 1.8 to 68 o/oo.

The distribution of copepods in the ponds is also influenced by availability of food and the presence of predators. In pond 1 free-swimming copepods are numerous during summer only at the inlet where phytoplankton is available in the current entering from the Bay. At the outlet, the only copepods in summer are unidentified harpacticoids which live among the macroscopic algae. As in pond 1, the copepods that had been present during winter in pond 2 disappeared simultaneously with the disappearance of *Stichococcus* in July.

In pond 3 during the winter *Acartia, Eurytemora, and Pseudodiaptomus* were all present in fair numbers. The populations decreased concurrently with development of large populations of larval fish (*Atherinops*) during June and July. The number of fish decreased in August and September, and the population of copepods, consisting almost exclusively of Pseudodiaptomus, increased greatly. (What appeared to be vast numbers of *Pseudodiaptomus* had a dry weight of 400 mg per cubic meter, or 1.8 lbs per acre of pond surface.)

Copepods enter pond 5, but do not maintain a population there, nor do they live in pond 6 where *Artemia* thrives. Copepods and *Artemia* utilize the same food (*Stichococcus*) but do not compete. Salinity tolerance limits copepods to early ponds, and presumably limits *Artemia* to later ponds.

(3) Isopoda. *Limnoria lignorum* Rathke lives on the pilings and gates of the floodgate at the Slough, but is not found farther on in the ponds. Not only is there little wood for it to attack, but the increased salinity is limiting to this wood-boring species (Kofoid 1921). Another isopod, *Sphaeroma pentodon* Richardson, has large colonies in the mud at the shore of pond 1 on both sides of the floodgate at the Slough, and in a restricted area at the inlet of pond 2.

(4) Amphipoda. Unlike the isopods, amphipods are numerous in the Alviso ponds. One species, *Corophium spinicorne* Stimpson, is the most prevalent arthropod in the second pond during summer and fall. Wherever macroscopic green algae attain a dense growth, they support large numbers of *Corophium,* which takes on an almost worm-like existence in the tubes it constructs as the algae decompose. All stages of *Corophium* live among the macroscopic algae. Fish, which are the chief predators on *Corophium,* presumably find it difficult to get at the prey either in the tangled masses of living algae, or later in the tubes constructed in the matrix of decomposing algae.

Another species of Amphipod in the ponds is a green gammarid, probably *Anisogammarus confervicolus* Stimpson, which is not as prevalent as *Corophium* and does not have its tube-building habit. It is present among the living macroscopic algae, but it disappears with the start of reduction in oxygen concentration when the algae reach shore and begin to decompose.

(5) Decapoda. The only decapod observed is *Hemigrapsus oregonensis* (Dana), which was collected along the west shore of pond 1 near the inlet, along the banks of Mt. View Slough between ponds 1 and 2, and near the inlet to the third

pond on the banks of Indigo Slough. It seems less an inhabitant of the salt ponds than of the neighboring bay.

(6) Insecta. Although more numerous in brines of higher salt content, two insects are numerous in the Alviso series. *Trichocorixa reticulata* (Guerin-Menéville) is a member of a genus of aquatic Hemiptera whose peculiar distribution has been reported by Hutchinson (1931). Adults are found in the ponds throughout the year. Although egg-laying is continuous during spring, summer, and fall, the greatest hatch of young is in spring. During April and May nymphs were predominant. From June on adults outnumbered the young stages, but nymphs were present through summer and fall.

Trichocorixa is present in all the Alviso ponds, but becomes most numerous in pond 5 where it is the dominant animal and practically free of competition. Neither copepods nor *Artemia* are present. Without any filter-feeding animal to utilize them, *Stichococcus* cells accumulate in pond 5 as a bottom film. Only *Trichocorixa* seems adapted to live under the conditions in this pond, and to take advantage of a rich food supply. *Trichocorixa* like all aquatic Hemiptera, does not use dissolved oxygen, but surfaces periodically to replenish its air bubble. Being independent of dissolved oxygen, and apparently impervious to hydrogen sulfide, it can tolerate the conditions that occur during the cycle of the sulfur bacteria in ponds 1 and 2.

The other insect of importance in the ponds is the salt marsh fly, *Ephydra millbrae* Jones. It is present in all the Alviso ponds, but unlike *Trichocorixa,* is not the dominant animal in any of them. In ponds subsequent to the Alviso series, really large populations of *Ephydra* may develop. Adults rise in swarms from the pond surfaces, and cast larval skins and pupal cases collect in drifts several inches deep.

The rat-tailed maggot of the drone fly *Eristalis tenax* Linnaeus is present at times in early ponds, but is more numerous in later ponds in accumulations of winter eggs of *Artemia* and pupal cases of *Ephydra.* The kelp fly, *Fucellia rufitibia* Stein, is often present on the surface of floating green algae, in the first two ponds.

H. Mollusca. (1) Pelecypoda. Lack of tidal action may be a factor excluding the mud mussel, *Modiolus demissus* Dillwyn, and the oyster, *Ostrea lurida* Carpenter, from the salt ponds. Both are present in the Slough but are not established in the ponds.

(2) Gastropoda. *Nassarius obsoletus* (Say), an east coast species probably introduced with oyster spat, is now the most abundant "mud snail" in San Francisco Bay. The west coast *Nassarius fossatus* Gould is apparently absent from the southern end of the Bay. MacGinitie and MacGinitie (1949) describe feeding habit and egg-laying of *N. fossatus; N. obsoletus* seems quite similar in these habits. Swimming larvae of *N. obsoletus* were taken in May at the outlet of pond 1, and the inlet of 2. Adults seemed to be excluded from the areas where large amounts of macroscopic algae decomposed anaerobically, and were most numerous where limited quantities of algae decomposed aerobically along the west shore of pond 1. *Nassarius* was present in the ponds up to the inlet of 3. In the areas of its limited distribution, *Nassarius* is the dominant bottom-dwelling organism.

I. Fish. The mud-sucker (or long-jawed goby) *Gillichthys mirabilis* Cooper, and the staghorn sculpin, *Leptocottus armatus* Girard, are present in the first three ponds, but only in limited numbers. The two fish of numerical importance in the Alviso ponds are the three-spined stickleback, *Gasterosteus aculeatus* Linnaeus, and the topsmelt, *Atherinops affinis* Ayres.

Adult *Gasterosteus* were present throughout the year in the first two ponds, where they were especially noticeable in the clear water above growing *Enteromorpha* in summer and fall. Although small sticklebacks (6-30 mm.) were present in pond 3 in late winter, *Gasterosteus* did not seem to thrive there when the salinity increased during summer and fall. Stomach contents indicated that during winter and spring, when copepods were available in the first two ponds, *Gasterosteus* fed on them. When copepods became scarce (after *Stichococcus* had been replaced by the macroscopic algae in June and July) *Gasterosteus* became more omnivorous, and picked off what amphipods and other animals it could obtain from the large algae.

The topsmelt *Atherinops* is the most numerous fish in the Alviso ponds. The eggs of *Atherinops* were collected at several stations in April. Spawning began in March and reached a peak in April and May when young fish in the yolk-sac stage (4-8 mm.) were predominant. Small fish (5 mm.) were still present in mid-August, but numbers were few after mid-May. By August a length of 80 mm. was attained, indicating rapid growth during the first four months; growth was slower during fall and winter so that by spring the length of spawing females was 100-110 mm. (For the size and growth rates of various subspecies of *Atherinops* on the Pacific Coast see Schultz, 1933.)

In the third of the Alviso ponds the salinity was between 39 and 41 o/oo in March and April when spawning began. Salinity increased to 45 o/oo in May and reached its maximum of 55 o/oo in October. *Atherinops* was able to withstand this range of salinity and to live throughout the year in pond 3 as well as in ponds 1 and 2. Possibly because of the lack of copepods it did not do as well as *Gasterosteus* in the first two ponds during summer and fall. In the third pond, however, *Atherinops* became the only fish present during the period of greatest salinity. It had a continuous supply of copepods there, since the equally salt-tolerant *Pseudodiaptomus* also thrived in pond 3 in summer.

Atherinops does not feed exclusively on copepods. The diatom, *Melosira,* may make up most of the stomach contents of young stages in pond 1. When copepods were scarce in pond 2, the stomach contents of *Atherinops* were green with plant matter. Filaments of *Rhizoclonium* and *Enteromorpha,* and especially the young shoots of the latter, were eaten in considerable quantity.

Atherinops does not survive in ponds 5 and 6. Individuals that enter them live for a time, feeding on *Artemia* (eggs, young, and adults), and on *Trichocorixa.* Although the fish did not reach maturity in the high salt concentrations of the sixth pond, *Atherinops* was observed to spawn there. The development of a school of young fish that hatched at the inlet of pond 6 and survived until a salinity of 90 o/oo was reached has been reported elsewhere (Carpelan 1955).

The numbers of *Atherinops* in the Alviso ponds were not estimated. In schools of young fish, which usually concentrated in regions of swifter currents, there have been as many as 1000 individuals per cubic meter. Other, larger, areas of the ponds may be devoid of fish.

J. Birds. Shore birds, preying on fish and to a lesser extent on *Artemia,* are the last link of food chains that start in the ponds. The extent of their predation was not estimated, and only the most numerous or conspicuous birds are mentioned below.

Great flocks of White Pelicans (*Pelecanus erythrorhynchos*) rest on the levees and the adjacent salt marsh. More limited flocks are present in the first two ponds where they feed on fish, principally topsmelt.

The Great Blue Heron (*Ardea herodias hyperonca*) and the Common Egret (*Casmerodium albus*) are conspicuous due to their size. They spear fish, and usually hunt alone; but they will congregate to available food as on one occasion when many of them lined the shore of a canal, gorging themselves on topsmelt that had been stunned or killed going through a pump between ponds.

Long-billed and Hudsonian Curlews (*Numenius americanus* and *N. hudsonicus*), Marbled Godwits (*Limosa fedoa*) and Willets (*Catoptrophorus semipalmatus*) are often seen in mixed flocks on the levees. Limited numbers of Least and Western Sandpipers (*Erolia minutilla, Ereunetes mauri*) feed on *Artemia* in shallow waters of later ponds. The American Avocet (*Recurvirostra americana*), one of the most numerous and the most vocal of the birds of the ponds, also feeds on *Artemia.* It can feed while floating but, like the sandpipers, is most often seen feeding in shallows where it can wade. Such an area is present near the outlet of pond 6 where there is usually a large population of *Artemia.*

Gulls are relatively few around the Alviso ponds, but mixed flocks, including the California Gull (*Larus californicus*) and the Ring-billed Gull (*Larus delawarensis*), are sometimes present on the levee near the inlet of the first pond.

The Caspian Tern (*Hydopogne caspia*) is a resident. Its eggs are laid on levees between other ponds lying a few miles to the north of the Alviso series. The Forster Tern (*Sterna forsteri*) is the principal predator on topsmelt. It circles and dives for them wherever they concentrate in schools, as at the inlets of the first three ponds.

Stichococcus

Stichococcus bacillaris Nägeli is a well-known organism, described in Smith (1950), that has been studied in laboratory culture by Eilers (1926), and by Ketchum and Redfield (1949), among others. In the Alviso ponds the cells are suspended singly without tendency toward filament formation. Reproduction is entirely by fragmentation. *Stichococcus* is so successful in certain of the Alviso ponds that its growth suppresses that of other algae. Since the usual size of its cylindrical cells is 4 by 7 micra, it is readily separated from larger organisms by filtration through paper. The filtrate is essentially a unialgal suspension of *Stichococcus* on which the following quantitative studies were made.

Seasonal changes in population

Method.—Light transmission by paper-filtered pond samples was determined with red filter (660 mu) in a Klett-Summerson instrument. The unit used in the following discussion is optical density (O. D.). Interference with light transmission due to turbidity or to difference in pigmentation or

cell size rather than cell number could not be ruled out; however, the method correlated fairly well with dry weight (see later), and provided a rapid method for following seasonal changes.

Results.—At the end of January, 1951, the clear waters of ponds 1 and 2 began to become green and opaque with *Stichococcus* cells. The lower (dotted) curve of Figure 8 shows the increase in optical density in pond 2 from February to a peak in April. The decline, beginning in May, continued until *Stichococcus* disappeared in August. The trend of population in pond 1 was similar to that illustrated for pond 2. In pond 3 (upper solid curve of Figure 8) the peak of bloom was in May and June. A smaller population was present from July through fall and winter. In pond 5 (dotted curve of Figure 9) the population attained in June was maintained, with fluctuations, for the rest of the year. In pond 6 (solid curve of Figure 9) the greatest density of *Stichococcus* occurred in the fall.

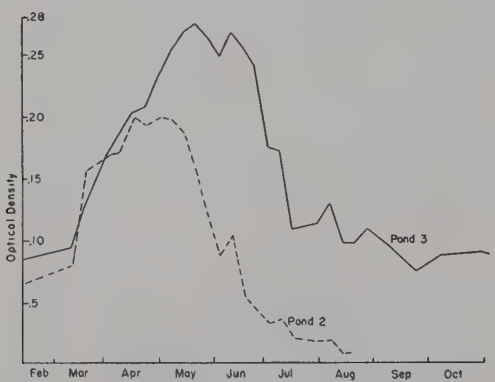


FIG. 8. Seasonal optical density, ponds 2 and 3.

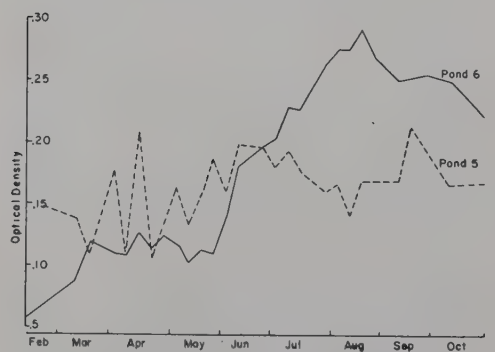


FIG. 9. Seasonal optical density, ponds 5 and 6.

Discussion.—In ponds 1 and 2 the population of *Stichococcus* decreased, coincident with decrease in nitrate concentration, prior to intake of water. When water began to flow into the ponds, the season (May) had advanced to the time when *Rhizoclonium* and *Enteromorpha* began vegetative activity and took up the nutrients entering from the Bay. Their competition, apparently, suppressed *Stichococcus* (see Marshall 1947). The small amounts of nutrients leaving pond 2 during summer and fall were sufficient to maintain a smaller population of *Stichococcus* in pond 3 after the spring bloom had depleted the larger amounts accumulated during the winter period of algal inactivity. The prolonged bloom in pond 3 (compared to that in ponds 1 and 2) was apparently at the expense of nutrients entering from pond 2 prior to attainment of maximum growth by *Rhizoclonium* and *Enteromorpha.* In ponds 5 and 6 there was a depletion of nutrients in spring. Nutrient concentrations and algal density increased during fall in pond 6 due to evaporation of water. *Stichococcus* cells from pond 3 and 5 flow into pond 6, where they concentrate in the fall. Figure 5 shows that the most rapid increaee in salinity occurred at the outlet of 6 from July to August which was the time when increase in density of *Stichococcus* also reached its peak.

Growth rate

During the bloom of *Stichococcus* in spring, the form of the curves of Figure 8 resembles the logarithmic phase of the typical logistic curve. Logarithmic rates of growth of various unicellular algae in culture have been reported to range from 0.4 to 0.85 $\log_{10}$ units per day (Myers 1951). The most rapid rate of growth observed for *Stichococcus* in the Alviso ponds occurred during the week from March 12 to 19. During this period the calculated growth rates were 0.045 $\log_{10}$ units per day in pond 1, and 0.041 in pond 2. The rates in the ponds are approximately 1/10 the rates for slower-growing algae in culture and 1/20 the rate of the most rapidly growing species.

Maximum rate of growth occurred in the ponds that had been without *Stichococcus* during fall and winter, so that there were small initial populations in water with relatively high concentrations of nutrients. In later ponds, which had higher initial populations in early spring, the increases in the populations were slower and extended over longer periods of time.

The remaining sections on *Stichococcus* deal with its productivity.

Dry weight of standing crop

Method. Samples were concentrated by centrifugation, evaporated to dryness and weighed.

Correction was made for salt content. Weight correlation with optical density was roughly 1 gm/liter/unit of optical density. For example, a pond sample with the low optical density of 0.096 contained 0.091 gm. of *Stichococcus* per liter. Samples with the relatively high optical density of 0.24 contained 0.24 gm. of *Stichococcus* cells per liter.

Results. During 1951 the average optical density in pond 3 was 0.17 which represents 0.17 gram per liter. Since the average depth is ½ meter, an acre of pond surface represents a volume of 2023 cubic meters. The average standing crop of *Stichococcus* in pond 3 was thus 85 grams per square meter (750 lbs. per acre). At the peak of bloom in pond 3 the standing crop was 1200 lbs. per acre. In pond 5 the average was 80 grams per square meter (700 lbs. per acre), and in pond 6, 97 grams per square meter (850 lbs. per acre). At the peak of population in August, the crop in pond 6 was 137 grams per square meter, or about 1200 lbs. per acre.

The annual production of *Stichococcus* in pond 1 and 2 was not estimated. The average standing crop of *Enteromorpha* in pond 2 was estimated to be 0.3 gm. (dry weight) per liter, which is 150 grams per square meter (1300 lbs. per acre).

Kjeldahl nitrogen

Method.—Kjeldahl nitrogen was determined by a technique made applicable to sea water by Robinson and Wirth (1934).

Results.—Total Kjeldahl nitrogen ranged from as low as 86 μg-A/1 in the first two ponds during summer to as high as 1037 μg-A/1 in pond 6 during fall. Dissolved Kjeldahl nitrogen, the portion present in Seitz filtrate, ranged from 55 to 70% of the total.

Discussion.—The total Kjeldahl nitrogen in the Alviso ponds is from 10 to 100 times greater than the total reported for the oceans (Moberg and Fleming 1934). In lakes and in the ocean, dissolved organic matter has been reported to exceed particulate organic matter in suspension as plankton (Bond 1933; Krogh 1934). In the Alviso ponds, the density of plankton is so great that the particulate fraction always exceeded the amount of dissolved Kjeldahl nitrogen.

Oxygen Production

Method.—Oxygen production was determined by the dark and light bottle technique, long used in field studies of productivity (Riley 1941). Its use in eutrophic waters seems justified according to data presented by Ryther and Vaccaro (1954). Water samples in duplicate one-liter bottles were suspended just beneath the surface and exposed for 6 to 8 daylight hours to the conditions of light and temperature prevailing in the ponds. After exposure, concentrations of dissolved oxygen were determined by the Winkler method.

Results.—In Table VI are shown seasonal changes in oxygen production and optical density in ponds 2 and 3. In pond 2 decrease in hourly rate of oxygen production paralleled the disappearance of *Stichococcus*. In pond 3 oxygen production was greatest during the upward trend of the population curve in May (Fig. 8). An equal population in June (Table VI) produced less oxygen. During the period with relatively stable population after July, the hourly rate of oxygen production in pond 3 followed the size of the population more closely than it did during the period of decline of the bloom.

TABLE VI. Optical density and oxygen production, ponds 2 and 3, 1951

Date	Pond 2		Pond 3	
	Optical Density	O_2 Prod'n (ml/1/hr)	Optical Density	O_2 Prod'n (ml/1/hr)
May 7	0.2	1.3	0.25	2.1
June 19	0.05	0.43	0.26	1.4
July 2	....	....	0.17	1.4
July 30	0.02	0.17	0.11	1.37
Aug. 13	0.01	....	0.10	0.99
Oct. 9	....	....	0.086	0.83

Data from dark and light bottle tests in pond 5 and 6 also indicate that size of population is not a good index of algal productivity. Table VII shows that a small active population at the inlet of pond 3 produced as much oxygen as a much larger population at mid-pond 6. At the outlet of 6, where *Stichococcus* is near the upper limit of its range in the salt ponds, oxygen production by the large concentration of cells was very low.

TABLE VII. Optical density and oxygen production, ponds 3, 5, and 6, August, 1951

Location	Optical Density	O_2 Prod'n (ml/1/hr)
Pond 3 Inlet	0.07	1.0
" 5 Inlet	0.145	0.8
" 5 Midpond	0.17	1.25
" 6 Midpond	0.22	1.0
" 6 Outlet	0.29	0.65

Daily rates of oxygen production for all seasons are not available for all ponds. For pond 3 results of dark and light bottle tests at various times of the year allow an estimate of daily oxygen production. From data shown in Table VIII it was

calculated that the average daily assimilation of carbon was about 3.9 mg/liter, with a yearly production of about 1400 mg. of carbon per liter.

TABLE VIII. Seasonal carbon assimilation, pond 3.

Month	Average Daily Oxygen Prod'n (ml/1/day)	Calculated* Average Daily Carbon Assimil. (mg/1/day)	Calculated Av. Monthly Carbon Assimil. (mg/1/month)
April.....	12	6.4	192
May.....	17	9.3	280
June.....	10	5.4	162
July.....	8.5	4.6	138
August.....	7	3.8	114
Sep. to March...	4.5	2.4	504/7
			1400/yr.

*12/22.4 = 0.536 mg C/ml CO_2
Assuming one ml of CO_2 assimilated per ml of O_2 evolved, 0.536 mg of C would be assimilated per ml of O_2 evolved.

Discussion.—Riley (1941), using a similar dark and light bottle technique, found in the waters of Long Island Sound an average carbon assimilation of 0.175 grams per cubic meter per day, and estimated a yearly production of 64 grams of carbon per cubic meter at the surface. He estimated that 600 to 1000 grams were assimilated yearly under one square meter, assuming 10 to 15 meters to the compensation depth. Since pond 3 averages only ½ meter in depth, the production of 1400 grams of carbon per cubic meter per year would be 700 grams per square meter of surface. The productivity of the pond and of the Sound thus seem to be about equal on the basis of surface area, but the production in the salt ponds is accomplished in 1/20 to 1/30 of the volume.

Although highly productive compared to coastal sea water, the productivity of *Stichococcus* in the Alviso ponds is far below productivity obtained in algal culture. The carbon assimilation in pond 3 was estimated to average 1.4 grams per liter per year. Assuming carbon to make up half the weight of naturally green algae, about 3 grams of organic matter are produced per liter per year. Converted into short tons, this amounts to a production of 6½ tons per acre per year.

In contrast to this rather low production, Milner (1955) has estimated that at the latitude of the Alviso ponds, on the basis of the best experimental conversion of light energy into plant material, it would be theoretically possible to obtain 120 tons per acre per year. The best efficiency in laboratory cultures of *Chlorella* has been considerably less than the theoretical figure, being 40 tons per acre. Various factors in nature seem to limit production in the Alviso ponds to about 1/6 the best laboratory yield. Laboratory studies, to be reported elsewhere, indicate that productivity of *Stichococcus* in the Alviso ponds may be limited by suboptimal concentrations of available carbon in the alkaline sea water medium, as well as by suboptimal concentrations of N and P.

SUMMARY AND CONCLUSIONS

A series of five salt-producing ponds along the shores of San Francisco Bay, California, was the subject of an ecological survey. Salinity increases in successive ponds as brackish bay water evaporates as it flows through the ponds. Mean annual salinity ranges from 27.5 o/oo in the first pond to 93.5 o/oo in the sixth. The pH of the first three ponds is very high (the summer mean is 9.5), but in later ponds, with salinities above 80 o/oo, pH is lower and nearly constant at 8.1. The extreme annual range of temperature was 25°C. (8° in January to 33° in August). Mean water temperatures are far above that of adjacent marine areas. Most of the area of the ponds is well-oxygenated, but there is a wide diurnal range of dissolved oxygen. Limited areas become anoxic during putrefaction of green algae. Relatively high concentrations of plant nutrients, which enter with water from the bay, are assimilated by macroscopic algae in ponds 1 and 2. Nutrients are not available to later ponds until bacterial action releases them from organic combination.

The principal plants of the first two ponds during summer and fall are filamentous green algae, *Rhizoclonium* sp. and *Enteromorpha* sp. They alternate seasonally with a single-celled green alga, *Stichococcus bacillaris,* which is present only in spring in the early ponds, but is predominant throughout the year in ponds 3 to 6. Many invertebrate phyla of animals are represented in the ponds, but other than Arthropods only the mud snail, *Nassarius obsoletus,* and a polychaete worm, *Polydora ligni,* are present in number, and both are restricted to ponds of low salinity. In the first two ponds *Corophium spinicorne* is the principal amphipod, and *Acartia tonsa, Acartia clausi,* and *Eurytemora hirundoides* are the main copepods. In the third pond, although the other copepods may occur during winter, *Pseudodiaptomus euryhalinus* is the only copepod present in summer. It tolerates salinities up to about 60 o/oo. The principal animal of pond 5 is an insect, *Trichocorixa reticulata,* which is also present in pond 6, but is insignificant there compared to the numbers of brine shrimp, *Artemia salina.* In the first two ponds the stickleback, *Gasterosteus aculeatus,* is the most prevalent fish. *Atherinops affinis,* the topsmelt, is the only fish able to tolerate the conditions in pond 3.

The average standing crop of *Stichococcus* in pond 3-6 was estimated to be 170-190 mg. of organic matter (dry weight) per liter. Its assimilation, based on oxygen production, averaged 3.9 mg. of carbon per liter per day, for a yearly production of 6.5 tons of organic matter per acre. Maximum growth rate, during a spring bloom in ponds 1 and 2, was about 1/10 that reported for slower-growing species of single-celled green algae in culture. Productivity of *Stichococcus* in the Alviso ponds was estimated to be about equal, per unit of surface area, to estimated production reported for coastal sea water, but productivity is 20 to 30 times as great per unit volume.

The first two of the Alviso ponds, having a salinity range from 23 to 38 o/oo, cover the salinity spectrum from poly- to ultra-haline regions of proposed classifications of brackish water (see Hedgpeth 1951). Faunistically they are polyhaline, with *Enteromorpha, Rhizoclonium, Polydora, Corophium* and *Gasterosteus* as typical organisms. In algal flora they resemble Scottish lochs (Marshall 1947), but, especially in lack of tidal action, the Alviso ponds are not estuarine. Other factors (including shallowness, variable concentrations of dissolved oxygen and of nutrient salts, great temperature range, and high pH) are probably as important as salinity in making the salt-producing ponds more similar to littoral lagoons (D'Ancona 1954) than to estuaries. In many of their environmental factors the first two of the Alviso ponds resemble salt marshes (Nichol 1935) and such regions as the Sivash area of the Sea of Azov, described by Zenkevich (1947).

Pond 3, with a salinity range from 40-53 o/oo, can perhaps be considered meta-haline. Only the three most hardy of the organisms present in previous ponds tolerate the conditions. They form a complete food chain: *Stichococcus* eaten by *Pseudodiaptomus* which is eaten by *Atherinops*. Pond 3 is in the salinity range considered by Day (1951) who concluded from a study of South African estuaries that there is no peculiar hypersaline fauna, and that organisms living in a salinity of 40 to 60 o/oo are merely forms of unusual tolerance. Starting with pond 5, and more clearly in pond 6, conditions in the Alviso ponds become similar to inland salt lakes. Although insects, which together with *Artemia* are considered to be typical of salt lakes, are present in all of the Alviso ponds, only in pond 5 does an insect *Trichocorixa*, become the predominant animal. Pond 5 (salinity 50 to 86 o/oo) seems a transition region, not occupied by any of the organisms of marine origin, and yet not like pond 6 in which *Artemia* predominates.

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THE ORIGINAL FORESTS OF THE GEORGIA PIEDMONT[1, 2]

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Many writers have indicated that hardwood types were the climax forest in the Piedmont generally, and that pine is thus only temporary. Early settlers in the Georgia Piedmont (Fig. 1) soon changed the original forests into cotton fields and developed a prosperous agriculture. Since then, four major periods of land abandonment have resulted in a province characterized by "old-field" pine.

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[2] The helpful advice and criticism of Dr. Henry F. Perkins, Assistant Professor, Department of Agronomy. University of Georgia, is gratefully acknowledged.

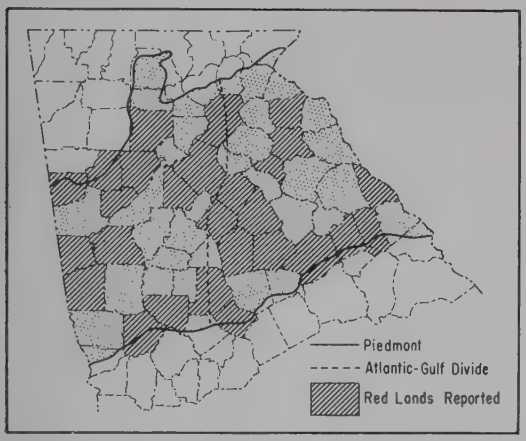

FIG. 1. The Georgia Piedmont, showing counties from which correspondents list timber species on the red lands (Loughridge 1883).

A pine forest economy has become established in the Georgia Piedmont. At first, it consisted primarily of the lumber industry, but since World War II, the pulp and paper industry has become a major element in the purchase of pine timber and Piedmont land. Heavy capital investments are now based upon perpetuation of pine timber types.

The pine economy is being threatened, however, by annual increases in hardwood acreage at the expense of pine. This paper is a detailed report on the composition of the original forests in the Georgia Piedmont prior to cultivation. It gives background for much current activity in attempts by landowners to counter natural succession.

Several recent papers point out the rapidity of succession from present pine types to hardwoods. Brender (1955), studying reproduction on the Hitchiti Experimental Forest in Jones County, on a limited acreage, found that 81 percent of the area had understory hardwood invasion. Wahlenberg (1949) surveyed 21 sample counties in the Piedmont of South Carolina, Georgia, and Alabama in 1946. He suggests that only a small proportion of "old-field" young pine will reproduce itself and that the trend of natural succession is from pure pine to complete invasion by hardwoods. He states: "Without it (cultural assistance) the pines probably cannot reclaim more than half the area being released by present cuttings."

An indication of the original forest composition can be obtained from a study of virgin forest stands located in representative soil formations in many regions. Unfortunately, the Georgia Piedmont has few such areas available. Bond and Spillers (1935), discussing the lower Piedmont (La Forge 1925), i.e. the 35 counties located just north of the fall line, estimated that more than four-fifths of the region had been cleared at one time or another. White, in his "Statistics of the State of Georgia" (1849) indicates that some counties of the Georgia Piedmont had a much higher degree of cultivation. For example, in Putnam County:

"The county was originally laid off into lots of 202½ acres; and such has been the fertility of the soil, that in 1847 there was only one lot which retained its original growth."

Braun (1950), in her recent book, states:

"Virgin forest, as it was before the local appearance of the white man, is today completely lacking in the region. . . . Only the forests of the few situations unfavorable for cultivation, such as ridges, knolls, and stream bluffs, and the occasional small tract on the better sites which has escaped clean cutting for cultivation remain, although even these have been selectively cut for generations."

Early Forest Conditions

The earliest records of Georgia Piedmont vegetation date back to the travels of Desoto in 1539. Dockstader (1928), in studying the diary of Rodrigo Ranjel, private secretary of Desoto, cites a description by Ranjel of the Indian village of Talimeco near Augusta on the Savannah River. He states that the people had many fine fields, a pretty stream and a hill covered with walnuts, oak trees, pines, live-oaks, groves of "liquid amber," and many cedars. Evidence from other writings of a later period (Barrett and Downs 1943) indicates that the walnuts were probably hickories.

Bartram (1791) in 1773-74, provided an excellent description of the early Georgia Piedmont. According to Harper's (1943) commentary on Bartram's travels, Bartram journeyed from Wrightsborough, then the last settlement at the edge of the wilderness, to the "Great Buffalo Lick" in southeastern Oglethorpe County, to Clarke County, to Madison County, and finally along the Great Divide to the north branch of the Broad River.

East of the Great Buffalo Lick, Bartram lists the forest trees as "Black, White and Red Oak, Hickory, of various species." With reference to the area west of the Little River, he states:

"The next day rode about 15 miles passing through for the most part of the way, a levell plain, Open Forest, generally Pine, mixt with Red and Black Oak and Hicory."

"We came into an open Forest of Pines, Scrub White Oaks, Black Jacks, Plumb, Hicory, Grape Vines."

The tax returns of 1788 (Raper 1943) in Greene County provide one of the few early quantitative references to timber types. John Swepson, the largest landowner in the county, declared 7,294 acres of which 5,519 were listed as "oak and hickory land" and 1,775 as "pine."

Some of the most descriptive accounts of the timber and other vegetation about 1800 are found in the letters of Benjamin Hawkins, the United States Agent for Indian Affairs South of the Ohio River (Georgia Historical Society 1916). In his earlier days as Indian agent, he made meticulous and detailed notes of his travels, describing the vegetation, topography, and Indian villages. For example, near the Indian town of Coweta, located about 2 miles below the present city of Columbus, Georgia, Hawkins described the vegetation at the fall line:

"The lands on the left bank of the river flat, and for some distance back, the timber pine, oak, hickory, the soil stiff. On the right side from the lower end of the falls up the river, a pine barron to the water's edge, the pines small."

Unfortunately, Hawkins' writings are difficult to follow because he continually refers to Indian names, towns, and geographic features. A thorough digest of his letters would require a separate work in itself.

The travelers of the early 1800's had little new information to add to the work of Bartram although the writings of several indicate a considerable knowledge of trees and taxonomy. Peter A. Remsen, a native of New York of Dutch descent, traveled across the State in 1817-18 and recorded his observations (Hesseltine and Gara 1953). However, his trip so closely followed the fall line that it is difficult to separate vegetation by physiographic province. A year or so later, Mr. Francis Gilmer, a friend of Thomas Jefferson and evidently an astute taxonomist, visited the Georgia Piedmont and did considerable botanizing (Davis 1943).

Other early literature substantiates the existence of pine, pine-hardwood, and hardwood types of forests in the Georgia Piedmont. White (1849), one of the earliest geographers in the State, made the following statements:

"The middle region of the State contains the oak and hickory lands, the soil being of a red, rich, loamy character. . . ." In Coweta County, "There are strips and patches of pine land, interspersed throughout the county, which are valuable for furnishing lumber. The main body of the county, however, is oak and hickory." In Heard County, "About one-third of the county consists of rich oak and hickory land; two-thirds are pine mixed with oak and hickory, . . . All the lands rest upon a good clay foundation." In Upson County, "The red lands are adapted to grains particularly. The pine lands are inferior."

A special Finance Commission of the State of Georgia received a statement concerning land evaluation from the Comptroller General's Office covering the year 1838 (Chappel 1874). The land, for evaluation purposes, was classified as 1st, 2nd, and 3rd qualities and Pine Land. Excluding the data from Habersham County because of the rather obvious discrepancy from the other estimates,[3] the percent of Piedmont in Pine Land was estimated at 15.4 percent in 1838.

Different tax rates were applied to the various qualities of land:

	Average tax
1st quality[4]	9-5/8 mills per acre
2nd quality	5-6/8 mills per acre
3rd quality	2-1/3 mills per acre
Pine lands	1-6/8 mills per acre

There is a good possibility that the estimates of pine land (Fig. 2) are higher than the actual condition because of the relationship of this listing to tax rates. This survey provided information to use in revising the tax system, the State being in dire straits at the time. A thorough search of the literature indicates that this survey is the earliest documentation of land within the State of reasonable accuracy.

Chappell (1874), in speaking of the pine barren speculation in Georgia, points out one basis for evaluating land around 1838: "They cause the different kinds of trees indicative of a rich soil, such as the oak, the hickory, the walnut, dogwood, buckeye, etc., to be entered as corner and station trees on the maps of the surveys."

From a survey of the 35 counties immediately north of the fall line in 1930, Bond and Spillers concluded that 10 per cent of the forest area in the lower Piedmont was in an upland pine type. They defined the type as including only upland forested tracts that had never been cultivated and contained shortleaf pine, loblolly pine, and hardwoods. They further state that shortleaf usually predominates over loblolly in the stands, but hardwoods may predominate over both. Most of the stands in this type were confined to the dry ridges and

[3] Habersham County had 61.3 percent of its lands listed as Pine Lands. The next highest figure is 28.6 percent. Other authorities (Loughridge 1883, White 1849) make no mention of Pine Land in what was then Habersham County.

[4] There is no definition of various qualities of land in the charge to the Comptroller General or in his original report (1839).

steep slopes. Their pine-hardwood type represented 11 percent of the forested area of the lower Piedmont and included fast-growing mixed pine and hardwoods found upon second-bottom and branch-head sites, mostly in uncultivated situations. This is the only reference encountered to an intimate mixture of pine and hardwoods on moist sites.

Wilson (1914) colorfully adds to the literature in his description of size of the timber in his anecdotes concerning Jackson County:

"Trees having a diameter of from six to nine feet, and a spread of branches of one hundred feet from side to side were not uncommon. Most of these were chestnut trees. . . ."

"Next in size came the poplars and white oaks, the latter often producing enough of big plump acorns to make it a difficult matter to walk over the ground where they had fallen. The length and size of their branches were amazing. They generally grew horizontal to the main body of the tree. This afforded bears and panthers a favorite lurking place. The poplars were not so numerous as the oaks but some of them grew to an immense size. Near the junction of big and little Sandy creeks stood a poplar that at the height of a man's head measured nine feet and seven inches in diameter. It was hollow, and about 1837 was cut down by raccoon hunters at the cost of the lives of three valuable dogs and several raccoons, besides William Rhodes, one of the hunters, was crippled for the remainder of his life. Being a shoemaker by trade, he made a full set of lasts and the arm pieces of a pair of crutches out of a part of that big tree."

"Taking these prominent features, together with the great number of large and beautiful pine trees whose towering trunks overtopped all others. . . ."

Janes (1876) gives a further indication of the quality of Piedmont hardwoods—"in portions of Middle and Northern Georgia, there is still (1876) an abundant supply of hardwood lumber, suitable for manufacturing Railroad-Cars, Wagons, and Agricultural Implements, besides a great variety suitable for manufacturing furniture; . . .".

There is not much indication of disease or insect problems in the early days except for the diseases of chestnut. However, Stevens and Wright (1901) add an interesting sidelight: In Putnam County around 1900, "In many places the oaks are dying from bugs or worms boring into the trees near the roots."

Brender (1952) emphasizes an important point in his historical discussion, i.e.: the distribution of original forest and land types is not uniform throughout the Georgia Piedmont. He points out that over 75 percent of the lower Piedmont is made up of the red lands which perhaps supported an oak-hickory climax at the time of settlement. This proportion probably does not hold for the entire Georgia Piedmont.

Smith (1900) provides the best specific example of the general tendency in the early literature to mention pine more frequently in the western Piedmont counties than in the eastern. He describes the original forest in Elbert, Jackson, Clarke, Baldwin, Putnam, Morgan, Jones, and Jasper counties east of the Ocmulgee River and does not mention pine in a single statement.

West of the Ocmulgee, in describing the settlement of the lands opened around 1830, Smith states:

In Monroe County, "It does not differ from other middle Georgia counties, and, as is common in them, it has fine red land, rich bottoms and some gray thin land, and in the northern part a considerable pine belt."

In Fulton County at the site of the present city of Atlanta, "in an unbroken forest of oaks, hickories, and chestnut, in which there was quite a quantity of pine timber."

In Heard County on the Alabama border, "The western part of the county was a great pine forest. . . ."

The report of the commissioners to Chappell in 1839 also substantiates this conclusion (Fig. 2).

The general tendency of pine to increase in prevalence in the original forest stands from north

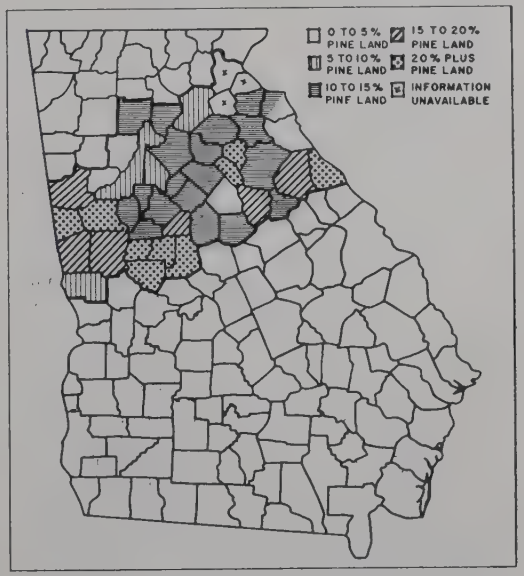

FIG. 2. Percentage of pine land in the Georgia Piedmont from estimate in 1838 (Chappell 1874).

to south is brought out by Stevens and Wright (1901) in their description of original forests incidental to county descriptions. Dawson, Hall, Clarke, Greene, and Putnam counties provide an example of the increase in pine toward the south.

In Dawson County, "oak of the various kinds, hickory, cedar, poplar, chestnut, locust, gum, walnut, mountain birch, and pine. Thus there is abundance of hardwoods for manufacturing purposes."

In Hall County, "mostly white oak, post oak, poplar, hickory, pine, maple, ash, walnut, mountain oak, and locust."

In Greene County, "Pine and the various hardwoods are found in the forests."

In Putnam County, "original forest, the growth of which is shortleaf pine, oak, hickory, gum, poplar and ash."

Again, the report to Chappell substantiates the conclusion of Stevens and Wright that pine was more prevalent in the southern than in the northern Piedmont (Fig. 2).

Specific Land Types

The original occurrence of pine and hardwood types within individual counties was a function of physiography and soil parent material. Land types mentioned in the literature can best be classified into four general groups:

1. Red lands, including mulatto or chocolate-colored sands and clays.
2. Flatwoods.
3. Gray, sandy and gravelly soils.
4. Granite lands.

In addition, specific references to the timber types of the bottomlands were found.

The red lands

Loughridge (1883) has a number of excellent citations regarding the timber of the red lands.[5] In a general statement concerning the red lands of the Georgia Piedmont, he states:

"The growth is red or Spanish, white, and post oaks, hickory, chestnut, dogwood, and some short-leaf pine. . . . The proportion of hickory is much larger, and that of pine much less, than on gray sandy soil."

Loughridge, in his report, includes correspondence from local people in 27 different counties with red lands (Fig. 1). Less than half mentioned pine as present on the red lands. Of those citations that do mention pine, it is listed as the last species in the association in nearly all cases. The several examples below serve to illustrate the relative unimportance of pine on the red lands:

In Haralson County, "The growth is hickory, oak, chestnut, poplar, dogwood, buckeye, persimmon, and black gum."

In Morgan County, "The red lands have a growth of oak, hickory, chestnut, poplar, gum, ash, and persimmon."

In Douglas County, "The red and mulatto lands differ from the gray in having sometimes walnut but little pine."

In Newton County, "The red clay uplands . . . the growth is post, red, and black oaks, hickory, and pine."

White (1849) substantiates the observations of Loughridge's correspondents:

In Henry County, "The mulatto or hickory lands are productive. . . ."

In Lumpkin County, "The hickory and oak lands have a mulatto soil. . . ."

Derry and Wright (1904) summarize as follows:

"In the forests of Northeast and Middle Georgia are found in the red lands, Spanish, white and post oaks, hickory, chestnut, dogwood, persimmon, sassafras. . . ."

Janes (1876) mentions pine in the red uplands of the western portion of the Georgia Piedmont. In Muscogee County, he describes the red uplands as having a growth of hickory, red oak, and pine.

Smith (1882), in describing the forests of the red lands in the metamorphic region of Alabama, adds an interesting fact:

"Its natural growth consists of the various species of oaks (white, post, Spanish, red and a few black-jacks), hickory, poplar, and some short-leaf pine, especially where the red and gray soils overlap, making mulatto-colored soils."

Using Loughridge's (1883) estimates for the occurrence of other land types, the residual acreage of red land amounts to 38 percent of the land area of the Georgia Piedmont. Roughly, this would include the eroded Cecil (both naturally and through cultivation), Davidson, and Lloyd soils.

The flatwoods

The Piedmont flatwoods or "glades" comprise but a small area in Georgia. Estimates are that 2 to 3 percent of the Piedmont is in flatwoods.

[5] Harper (1907) commented on Dr. Loughridge's work in 1907; "Quite a number of descriptions of the natural features of the whole State and its geological subdivisions have been published, but all prior to 1880 are superseded by Dr. R. H. Loughridge's report on cotton production (modestly so called) in the sixth volume of the Tenth Census Reports. . . . Taken as a whole, Dr. Loughridge's descriptions of the natural features of Georgia have never been surpassed for accuracy and completeness, and are not likely to be very soon.'

The belts are small and localized, occupying in the neighborhood of 30 to 50 square miles.

Loughridge (1883) states that in Elbert County, the flatwood's growth is blackjack oak. In Oglethorpe County, he mentions the blackjack flatwoods and in Jasper County, "the glade lands . . . have a growth of black-jack, post oak and hawbushes."

The gray sandy and gravelly soils

The gray sandy lands of the State, other than the Elberton granite formation, occupy approximately 46 percent of the Piedmont, according to Loughridge. Data from his correspondents indicate that the entire area of gray lands is approximately 60 percent. He separates out 14 percent of these as "granitic lands."

Loughridge states that the growth on the gray, sandy lands is "generally short-leaf pine, post, Spanish (red), and white oaks, hickory, dogwood and persimmon. . . . Pine has not as large a growth as on granite lands and only the short-leaf variety is found."

In nine out of fourteen counties, where the "granitic lands" were absent, the correspondents of Loughridge listed pine as one of the leading species. In several counties bordering the sand hills, however, the absence of pine was noted in the descriptions. Examples of the correspondent's reports are:

In Cobb County, "a sandy loamy soil . . . having a growth of pine, post, red and white oaks, and hickory, poplar, and beech."

In Carroll County, "The light sandy uplands with pine, oak, and hickory growth."

In Upson County, "The gray lands have a growth of pine, hickory, black-jack, post and white oaks."

In Coweta County, "with a prominent growth of long- and short-leaf pine, and oaks, chestnut, and hickory."

In Morgan County, "the gray lands, having a growth of oak, hickory, chestnut, persimmon, and pine."

The gray sandy lands discussed by Loughbridge are probably the uneroded Cecil, Appling, and Durham soils. The "eastern pine belt" and "western pine belt" described by Pinchot and Ashe (1897) in the North Carolina Piedmont are very similar to the gray sandy soils of the Georgia Piedmont.

Regarding the gray, sandy lands, Derry and Wright (1904) state that there is more hickory and less pine on the red lands than on the gray, sandy land. In contrast, Smith (1900) mentions the gray, post-oak lands in Jackson County with no reference to pine.

The granitic lands

The granitic lands, speaking primarily of the Elberton granite formation, cover about 2,600 square miles in the Georgia Piedmont (Loughridge 1883) or approximately 14 percent of the land area. They are localized in two principal sections: one is in Hart, Elbert, and Oglethorpe counties; and the other south of Atlanta characterized by granite hills. Stone Mountain and its outliers provide excellent examples of the latter.

There are several citations relating to the cover on this type of land. Loughridge himself states that "The almost universal timber growth on all these lands is pine (either long or short leaf), with oak, chestnut, hickory, and some black-jack." His correspondents do not mention timber types in such a manner that they can readily be correlated with the granitic lands, except in Putnam County. Robert C. Humber and J. T. Dennis of Eatonton divided Putnam County into three land types: deep-red clay lands, light gray lands, and light sandy pine lands. From the other descriptions, there is reason to believe that the "light sandy pine lands" are of granitic origin. They further state that "the light sandy pine soils cover but a small area in the county."

Watson (1902) produces several citations of pine stands on the granitic lands. With reference to the Flat-Rock Quarry in Heard County, a quarry site of 400 acres located three miles southwest of Franklin:

"Parts of the outcrop are well set, in a heavy growth of excellent pine timber. . . . A comparison of this analysis with analyses of the granite-gneisses from DeKalb, Gwinnett and Rockdale Counties shows very close agreement."

Again, in Heard County, Smith (1900) states:

"The western part of the county was a great pine forest, and had in it one of the largest quarries of monumental granite in the State."

The bottomlands

Although the bottomlands derive their soil characteristics chiefly from the adjacent uplands and are similar to them geologically, they were important enough in the early agriculture to warrant numerous citations in the early writings.

Loughridge's correspondents distinguished between bottomlands and stream bottoms. In the bottomlands, poplar, oak, maple, sweetgum, and walnut were the most frequently mentioned species. In the stream bottoms, sweetgum and poplar were most frequently mentioned and beech was noted in several instances—indications of

coves. Pine received little notice, e.g. "some shortleaf pine[6] . . . in the lowlands."

Derry and Wright (1904) cite lowlands in two instances:

"In the forests of northeast and middle Georgia . . . and, in the lowlands of some counties, short-leaf pine,[6] poplar, ash, walnut, cherry, and buckeye."

"Among the red hills throughout the section lying between the Savannah and Flint Rivers . . . with beech, maple, and poplar on the lowlands."

Janes (1876) describes the bottomlands in Muscogee County as "timbered with Hickory, White Oak, Poplar, Gum, Beech, and Walnut."

Summary and Conclusions

An examination of early literature concerning the species composition of the Georgia Piedmont forests prior to clearing and cultivation indicates that:

1. The forest composition ranged from virtually pure pine stands to pure hardwood stands including the range of mixtures (Fig. 3).

2. A small acreage, perhaps 2 or 3 percent of the land area, was in "flatwoods" with a black-jack oak stand.

3. Between 35 and 40 percent, the red lands, supported a forest composed of hardwoods with little or no pine. Obviously, these areas will be most difficult to maintain in pine.

4. Approximately 45 percent, the gray, sandy lands, had a mixed pine-hardwood forest cover at the time of settlement, varying in composition such that stands approached either extreme.

5. Some granitic lands, mostly of the Elberton formation and occupying 15 per cent of the land area, had predominantly a pine composition. It is concluded that most of the pure or predominantly pine stands at the time of settlement occurred on these granitic lands. Hardwood invasion will probably be least troublesome on these soils.

6. The proportion of pine was greater in the drier situations and less on the moister situations within a specific land type. For all practical purposes, pine was not present on the bottoms.

7. The distribution of original forest types was not uniform throughout the Georgia Piedmont, but in general the pine types and the stands with heavier portions of pine seemed more prevalent west of the Atlantic-Gulf divide than east of it. The percentage of pine types also seemed to decrease from the sandhills to the mountains.

[6] Early writers may have used the term "short-leaf pine" to distinguish both shortleaf and loblolly pine from longleaf pine. The common pine of the bottomlands in the southern Piedmont of Georgia is loblolly pine.

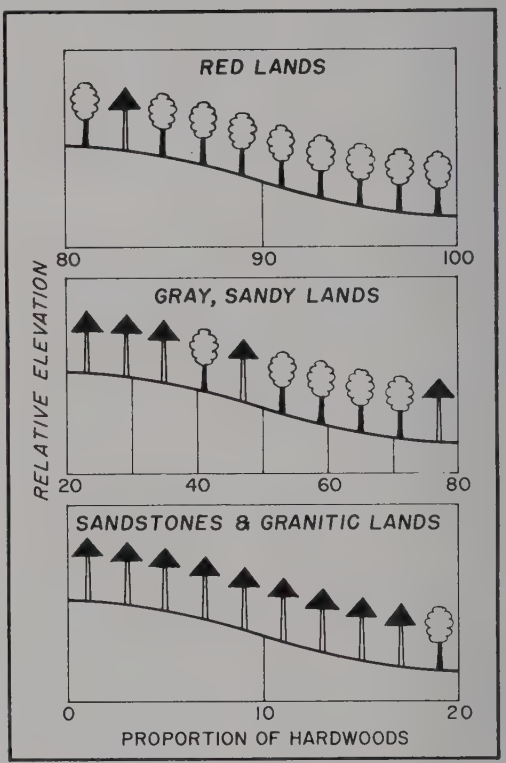

Fig. 3. Diagrammatic sketch of probable original forest types in the Georgia Piedmont as related to land types. The red lands supported predominantly hardwoods, the gray, sandy lands a mixture of pine and hardwoods, and the standstones and granitic lands predominantly pine.

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PHYTOSOCIOLOGY OF THE LARGER SUBMERGED PLANTS IN WISCONSIN LAKES[1]

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INTRODUCTION

This investigation was undertaken with the intention of increasing understanding of the sociology of submerged vegetation in Wisconsin lakes and with the hope that a system could be devised by which the communities of large submerged plants could be objectively described or classified.

Previous phytosociological work on aquatics has been inadequate to clearly demonstrate the nature of the communities. In Wisconsin, Rickett (1922, 1924) and Wilson (1937, 1941) divided the lakes they studied into natural areas and investigated the plants within them, but the zones they studied were so inclusive that the existence or non-existence of discrete, recurring associations cannot be determined from their data. The data of Olsen (1950a, 1950b) showed an overlapping of species distributions among the various water types in southwestern Jutland, Denmark. Although Olsen's papers did not discuss communities, his data on species distribution indicated strongly that the aquatic plant communities in southwestern Jutland were continuous variables rather than discrete entities. Moyle (1945) in a study of the distribution of aquatic plants in Minnesota found that "although three more or less distinct aquatic floras can be delimited, actually each species of aquatic plant has its own range of chemical tolerance and set of chemical conditions under which it makes its best growth."

The procedure employed in this investigation was a quantitative comparison of objectively chosen stands of submerged vegetation which were homogeneous enough to be considered as studiable

[1] The field work for this project was supported by the Lake and Stream Investigations Committee of the University of Wisconsin, with funds supplied by the University Research Committee.

units. Because of the large number of lakes in Wisconsin and the range of environmental conditions which they possess, the scope of the study was restricted by placing emphasis on the eutrophic lakes, i.e., those rich in nutrient substances. Figure 1 shows the locations of the lakes included in this study. Southwestern Wisconsin is unglaciated and contains few natural lakes. The vegetation studied included the submerged angiosperms and the Characeae. The presence of mosses in the communities was noted, but their frequencies were not included in calculations of relative frequencies in stands. Nomenclature follows Fassett (1940); voucher specimens are deposited in the University of Wisconsin Herbarium.

FIG. 1. Locations of lakes studied.

Lakes of Wisconsin

Acid crystalline rocks of Archaean origin underlie most of the glacial drift in northern Wisconsin, and limestones and sandstones of Cambrian, Ordovician and Silurian age underlie most of the drift in southern Wisconsin. Most of the natural lakes in the state are glacial in origin and the differences in bedrock and glacial deposits are manifested in differences in the character of the lakes' water and sediments.

The bedrock of the southeastern part of Wisconsin is, for the most part, covered with a mantle of glacial drift up to 400 feet in depth. Eighty-seven per cent of the drift in this part of the state is composed of local limestone and sand stone (Martin 1932). Since the sedimentary bedrock is also, in great part, calcareous, the water which feeds the southeastern lakes is rich in bicarbonates and has a sufficient amount of phosphates.

The lakes of northern Wisconsin occupy morainal basins and have sandy or gravelly shores except where encroachment by bog vegetation has taken place. The surrounding topography varies from steep and high shores to comparatively low shores. The acid crystalline bedrock would ordinarily be a poor source of nutrients for life in lakes. Any influence it might have, however, would be insignificant in view of the thickness of the glacial drift which usually covers it. According to Juday and Meloche (1943), it is 130 to 234 feet deep in the Trout Lake region (Vilas County). The newer, surface drift is non-calcareous but at depths beneath the surface varying from 35 to 200 feet, calcareous material of older drift has been found (Broughton 1941). Where the older drift comes close to the surface, it increases the hardness of the ground water, some of which feeds streams and may in turn be carried into lakes, thereby increasing their bicarbonate content.

METHODS

Selection of lakes

Relatively few of the thousands of lakes in Wisconsin could be investigated in this study, but an effort was made to include lakes of all the glaciated areas of the state. The criteria for the selection of lakes or parts of lakes for study varied somewhat with the purpose of the particular phase of the investigation involved. One criterion which applied to all decisions was that the lake or part of the lake to be sampled must be free or relatively free from disturbance. The following were the most common disturbance factors encountered: (1) bathing areas, (2) anchors from fishing boats, (3) in the southeastern district, carp, (4) deliberate mowing, raking, or poisoning of plants for the purpose of nuisance control, and (5) excessive accumulation of debris from land.

One other important criterion was applied to those phases of the investigation in which quantitative sampling was involved. It was deemed necessary to exclude areas which were strewn with large objects such as rocks and fallen trees which would make sampling by quadrat or rake inaccurate.

No attempt was made to select stands according to their chemical types. Instead a random sampling of stands was made, the number of stands in each area being somewhat proportional to the total number of lakes in the area. Thus the data obtained represented the vegetation and chemical properties of the type of lake predominant in each

area and the rare, exceptional stands were, by nature of the random sampling, poorly represented.

Selection of stands

One method for gaining understanding of the composition and structure of a type of vegetation is by division of the vegetation into stands, some of which may be individually analyzed and subsequently compared with one another. In order for a segment of vegetation to serve as a stand, it must belong to the type of vegetation under consideration and it must constitute a unit. The latter qualification implies that the stand be homogeneous in composition, within the expectations of random distribution or the degree of contagion inherent in the population.

The vegetational variation within a single lake is so great that the use of an entire lake as a stand is invalid. There are portions of lakes, however, usually opposite a uniform stretch of shore, where the littoral zone is apparently uniform in slope and, at any particular depth, in substrate and vegetation. Such an area will be referred to as a "community area." In this study, stands were delineated within community areas rather than entire lakes. However, the tendency for submerged communities to vary with depth also makes necessary a depth limitation for stands. Detailed work, which will be described below, revealed that in many community areas the vegetation along depth contours as little as one foot in depth apart was significantly different. It was also found that the vegetation along particular contours was, in the great majority of communities, uniform.

For this work, therefore, a stand was defined as the vegetation which occurs at a single depth in a community area, with a practical sampling error not exceeding six inches more or less than the depth of the stand.

Sampling devices

The most commonly employed method of sampling was the use of a weighted wooden frame with interior dimensions of 15 in. x 20 in. The quadrat was laid 20 times along the depth contour, with an error of 6 in. in depth. The length of the stand was approximated, and with allowance for edge effect, divided by 20 to determine the distance between quadrats. Then, maintaining the desired depth, the investigator walked the number of paces or swam the number of strokes equivalent to that distance, and dropped the quadrat. The inaccuracies inherent in these measurements modified the theoretical regularity of the sampling and introduced a modicum of randomness, or at least, irregularity.

The species present in each quadrat were determined by diving and inspection with the aid of a face mask. Recording was done either directly on mimeographed forms or, more often, on a wooden board from which on shore or in a boat, the data were transferred to the mimeographed form.

Preliminary experiments on two lakes in southern Wisconsin indicated that a 200 sq. in. quadrat would be adequate. In order to allow for the possibility of stands with sparser vegetation, a 300 sq. in. quadrat was decided upon. When the quadrat size is satisfactory, the dominant species are measured by high frequencies and the less common ones by low frequencies. As a means of verifying the quadrat size suggested by the preliminary experiments, the frequencies of the stands subsequently sampled by the 300 sq. in. quadrat were examined and it was found that the range in frequency values in most stands justified the size of the quadrate used. The stands in which a 300 sq. in. quadrat might have been excessive were those oligotrophic stands with mats of tiny plants such as *Eleocharis acicularis* and *Juncus pelocarpus f. submersus*. The rich stands with their large Potamogetons resembling underwater shrubs, however, discouraged the use of a smaller quadrat.

Frequently inclement weather or an unfavorable substrate discouraged the diving method. In such situations, a dandelion rake lengthened to eight feet by an extra handle was used instead of the quadrats. The functional part of a dandelion rake is curved and has wedge-shaped teeth. This type of instrument was found to be the most effective kind of rake and was successful in bringing to the surface the small plants often missed by an ordinary rake. The rake bottom was 15 inches long and was dragged through the upper part of the substrate for a distance approximated to be 20 inches. In order to equate the sampling by the two devices, the wooden quadrat was constructed with dimensions of 15 in. x 20 in. Thus the rake denuded an area of lake bottom the same size and shape as was delineated by the quadrat. Before actual use in sampling, much practice was taken in different depths of water and different types of substrate, until the ability to approximate with reasonable accuracy was acquired. Results were verified by diving and measuring the denuded area. Some stands were sampled by both quadrat and rake and the results were comparable.

Collection and analysis of water and soil samples

It has been demonstrated (Juday and Birge 1933; Olsen 1950) that electrolytic conductivity, i.e., specific conductance, measured in reciprocal megohms (mho x 10^6), is fairly well correlated with fixed carbon dioxide, pH, and calcium and magnesium content of surface fresh waters. Since it was not known which of these individual factors, if any, are most influential in plant distribution, conductivity was used as a general index of mineral richness of the water. Water samples were collected six inches below the surface in the vicinity of the plant beds investigated, and conductivity was measured with a conductivity meter.

Soil samples were obtained from the surface six inches at three locations in each stand and subsequently combined. The wet soil was air dried and then stored in paper bags. At the laboratory, the soils were ground to pass through a 2 mm. sieve, and the content of sand was approximated. Carbonate content was determined by hydrochloric acid treatment, and total organic matter and ash residue by ignition of the sample remaining after hydrochloric acid treatment and washing. The soils were analyzed for pH, available phosphorus, potassium, calcium, magnesium, nitrate, and ammonium by the Wisconsin State Soils Laboratory.

The Nature of Aquatic Plant Communities

Several studies were carried out to reveal or document the spatial arrangement of aquatic plant communities and their seasonal changes.

Diversity of communities within lakes

It is apparent to even a casual observer that most lakes are not homogeneous vegetational units, even at a single depth. Variation in hydrography, bordering terrestrial topography and land use, exposure to wind, and proximity to inlets or outlets are among the factors which result in the diversified environmental conditions often found in different parts of the same lake. It can be safely assumed that this diversity of environmental conditions is at least partially responsible for the different kinds of plant beds often recognized in a single lake.

Several studies were carried out to determine the extent of this variability. In one such study, five stands were sampled, each at the four foot contour, at five locations along the north shore of Ellen Lake in Sheboygan County. It is obvious from the data (Table I) that the plant communities in Areas I and II are alike. This is to be expected since they occupy the same community area opposite a gravelly hill. Areas III and IV are opposite a low area and have different communities from the preceding two. They are somewhat different from each other as well, both in their vegetation and substrates. Area V is occupied by a very different community, as might be expected from the high silt and organic content of its oozy substrate.

Table I. Variation in community composition around the shore of Lake Ellen, Sheboygan County. All stands were in water four feet deep

Stand	I	II	III	IV	V
Shore topography	hill	hill	flat	flat	cultivated hill
Substrate	marl	marl	marl	marl, org.	marl, org., silt
Species	Relative Frequency				
Najas flexilis	54	54	30	5	7
Chara sp.	46	46	48	43	15
Potamogeton pectinatus	..	..	9	14	22
P. illinoensis	..	..	13	11	..
Ceratophyllum demersum	..	..	..	8	..
P. Friesii	..	..	..	8	11
Myriophyllum exalbescens	..	..	..	11	44

These results are typical of those of all the studies made. The tendency of many limnological investigators to treat lakes as single vegetational units makes it advisable to stress here that at least in vegetation studies the diversity of community areas within individual lakes should be recognized.

Variation of community composition with depth

The pattern of vegetation within community areas was studied by two methods: sampling of stands at successively deeper levels, and the mapping of small parts of community areas. The first procedure was followed in nine community areas, and in some the vegetation was homogeneous through a depth amplitude of up to 4 feet. In most areas, however, a significant difference existed between stands separated by as little as 1 foot in depth. The question then arises: Are the differences truly related to depth, or do equally great differences exist in the plant distribution along a single depth contour in a community area? Regressions of species on depth support the former, but more conclusive evidence is available from two sources:

1. The quadrats sampled at each depth were divided into four groups of five adjacent quadrats, in the order in which they were located. The four groups from each depth were compared with one another and, with very few exceptions, were reasonably uniform in composition.

2. A small community area in each of two lakes was mapped, so that the structure could be represented in detail. For each map, an undisturbed area with a gradual, regular descent was selected. One of the areas mapped was in Sand Lake, Oconto County, and another one was in Jordan Lake, Adams County (Fig. 2).

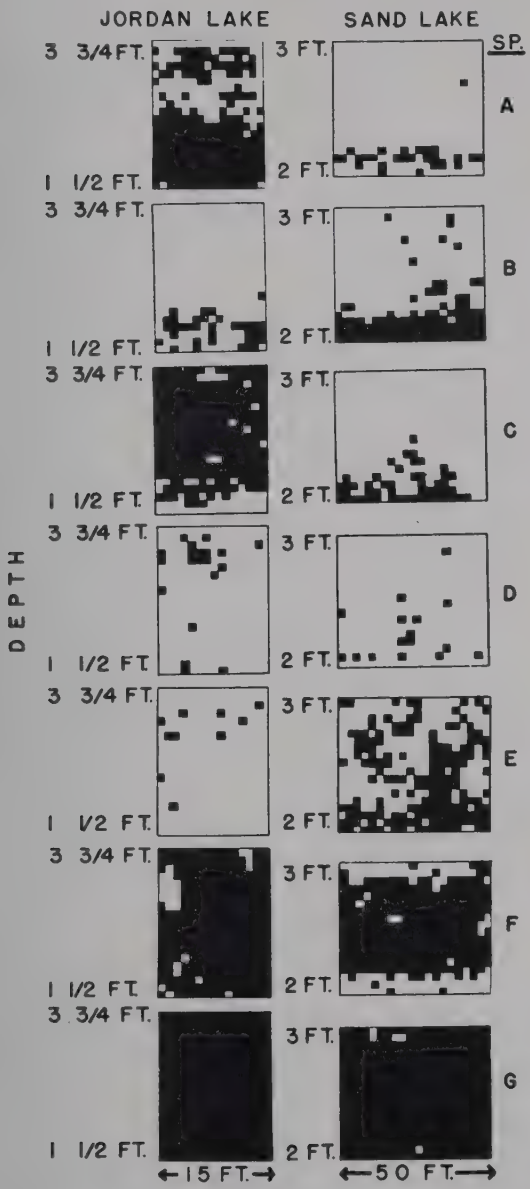

FIG. 2. Distribution of species in mapped areas of two lakes. Darkened squares indicate quadrats in which species was present. The species are: Jordan Lake: A. Sterile submerged *Sagittaria* sp., B. *Potamogeton pectinatus*, C. *Najas flexilis*, D. *P. amplifoliums*, E. *Myriophyllum exalbescens*, F. *P. gramineus*, G. *Chara* sp. Sand Lake: A. *Eriocaulon septangulare*, B. *Najas flexilis*, C. *Eleocharis acicularis*, D. *Juncus pelocarpus* f. *submersus*, E. *P. gramineus*, F. *Chara globularis*, G. *M. tenellum*.

All the species in the area mapped in Sand Lake, with the exception of *Myriophyllum tenellum*, whose depth amplitude in this location was greater than 1 foot, showed distinct correlation with depth, and a homogeneous distribution along contours. This was corroborated by Chi-squared tests. In Jordan Lake, however, marked correlation with depth was apparent only for *Potamogeton pectinatus* and *Najas flexilis*. The other species showed a more or less general distribution.

The difference in depth effect in the two areas is typical of the variability commonly encountered in aquatic vegetation. Both the map work and the successive contour work demonstrate that in certain areas the plant community composition remains essentially the same through as much as a four foot depth difference, at least insofar as frequency measurements are concerned. Even in such situations, however, tremendous changes in stature of the species often accompany changes with depth. Moreover, the prevalence of areas in this study in which a significant change in frequency composition accompanies a slight change in depth makes necessary a sampling system which adequately circumvents this problem.

Seasonal succession

In this region the quantity of non-planktonic large plants growing on the lake bottoms is greatly diminished in winter, and most species survive the cold period in the form of seeds, specialized winter organs, or pieces of stems or rhizomes which give rise to new shoots in the spring. An account of the vegetational changes which take place through the year in University Bay, Lake Mendota, was presented by Andrews (1946). According to Andrews, a change in species as well as quantity of plants takes place during the growing season. This presented a serious problem. Most of the sampling for the present investigation was carried out during late June and in July and August, 1952 and 1953, but if the early summer community in a given stand differed from the late summer community, all stands would have had to be sampled within a very short time interval if comparisons were to be valid.

The possibility existed, however, that the changes during July and August were changes in bulk and stature of the species, more than in frequency. In order to determine the importance of frequency change and the interval, if any, of fairly constant frequency conditions, six stands were each sampled two or three times during one summer.

Almost all the stands remained essentially the same in frequency composition from late June to middle or late August, 1953. Figure 3 illustrates the composition of a stand in Lake Ripley as sampled in June, July, and September 1953. The

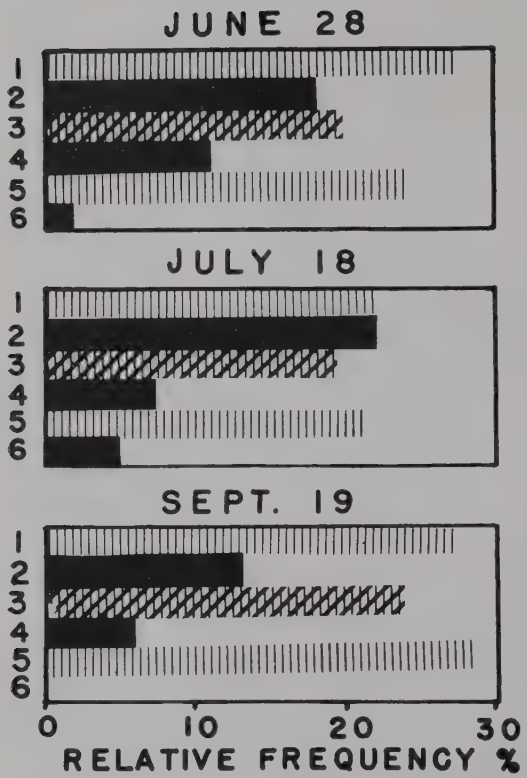

FIG. 3. Seasonal changes in a stand in Lake Ripley. The species are: 1. *Chara contraria*, 2. *Najas flexilis*, 3. *Potamogeton illinoensis*, 4. *P. pectinatus*, 5. *Vallisneria americana*, 6. *P. Friesii*.

results are representative of the results from other stands studied in this way.

Although these results appear to be inconsistent with Andrews' and with general observations, it should be noted that Andrews' work was based on wet and dry weights, and that ordinary observations are most influenced by the bulk of the plant matter. For example, Andrews stated that *Vallisneria americana* Michx. became the dominant plant in University Bay in August. However, he also said that the species was uniformly distributed over the bay, but that early growth was slow. *Vallisneria* is unimportant in July from the plant productivity viewpoint, but the small plants present at that time are just as effective in frequency data as are the large, conspicuous, fruiting plants of August. Similarly, plants which have their peak early in the summer and become inconspicuous later usually are then present in winterbudding, shredded, or otherwise degenerate form and may still be recorded for frequency purposes. Andrews' primary example of a plant which undergoes marked changes in the growing season is *Potamogeton crispus*. This plant is of no concern in the present study, however, because it is an introduced species which has thus far spread only slightly in Wisconsin.

It was concluded from the above studies that seasonal changes in aquatic plants do not affect the validity of the sampling methods employed in this investigation, within the limits of the time intervals during which the data were collected.

Ordination of Communities

Submerged plant communities are floristically poor, especially in comparison to the herbaceous vegetation of prairies and forests. Only 30 submerged plant species were found to occur more than rarely in the lakes examined, and the number of species per stand seldom exceeded eight. The description and explanation of their distribution, however, is not equally simple.

Various investigators in the past have correlated the distribution of aquatic plant species with certain environmental gradients. Manifestly, however, species are not distributed in a regular progression along the entire range of any single ecological factor; nor does a factor always have the same effect on the same species. An ecologically sounder concept is that distribution is affected by a complex of interacting environmental factors. Some of them, when present in excessive or limiting amounts, may be expected to have critical influence. Because the environment of aquatic macrophytes is so complex, the roles of the diverse environmental factors have not yet been sufficiently analyzed, and the effect of interactions among them on the plants is almost unexplored. It therefore appeared most advisable to utilize the plants themselves in an investigation of their sociology because they respond to the sum total of environmental factors. If the relationships of the plants to one another can be elucidated, it should be less difficult to analyze and synthesize the environmental influences. This approach was used, and this investigation was thus primarily a phytosociological one.

Most stands of submerged vegetation are composed of few species and the variability among stands is great. In order to ascertain the relationships among the species and stands, therefore, a method using association between pairs of species was preferred to direct comparison of stands by their total composition.

Five hundred and fifty-five quadrats from stands in 54 lakes were used in compiling an index of joint occurrence between species pairs. To

facilitate the compilation of these data, the species present in each quadrat were recorded on marginal punch cards. The total number of times each species occurred and the number of quadrats in which it occurred jointly with every other species was determined from the punch cards.

Nine of the 30 species occurred in less than 20 quadrats. Since such uncommon species would not be reliable in the formulation of a classification system, these were omitted from the early part of the procedure. An index of joint occurrence was calculated for the remaining 21 species. It was the number of quadrats in which two species occurred together expressed as a percentage of the number of quadrats of occurrence of the less common species. The occurrence of the less common species was used in order to avoid a low joint occurrence index for two species merely because one occurred infrequently. Subsequently the process was repeated using a different joint occurrence index in which the number of quadrats in which two species occurred together was expressed as a percentage of the average number of quadrats of occurrence of both species. Both indices when used in the manner described below produced the same groupings of species.

Species of pairs with zero joint occurrence were placed at opposite ends of a list, and species of pairs with high joint occurrence were placed near each other (Guinochet 1955). When the common species were so arranged, the rare species were easily inserted in the appropriate places. Eventually an order was obtained which is considered to be a reflection of the species' reactions to the complex of environmental factors. If the list is true to the natural ecology of aquatic plants, its application to an ordination of the communities they compose should result in a natural arrangement of communities.

The species were divided into four groups in the order of their positions on the joint occurrence list (Table II). The problem then presented itself as to how to assess a given stand so that its proportionate content of species in the four joint-occurrence groups could be properly represented. One method which has been employed for this purpose (Curtis and McIntosh 1951, Curtis 1956) is to weight the amount of each species in the stand (as measured in the field) by the number of the group in which it occurs and then sum the weighted values. For this purpose it is essential that the amounts be on a relative basis. When this procedure is followed, an index number is obtained for the stand whose magnitude is a reflection of all of the species composing the stand. Using this method in the present case, the number

Table II. Joint occurrence groups

1
Myriophyllum tenellum
Potamogeton epiphydrus
Juncus pelocarpus f. submersus
Elatine minima
Eriocaulon septangulare
Gratiola lutea
2
Potamogeton Robbinsii
Potamogeton praelongus
Sagittaria spp.
Potamogeton amplifolius
Isoëtes spp.
Myriophyllum alterniflorum
Eleocharis acicularis
Potamogeton gramineus
3
Potamogeton Berchtoldi
Vallisneria americana
Anacharis canadensis
Heteranthera dubia
Megalodonta Beckii
Najas flexilis
Potamogeton natans
4
Potamogeton pectinatus
Myriophyllum exalbescens
Potamogeton Friesii
Potamogeton Richardsonii
Ceratophyllum demersum
Potamogeton illinoensis
Potamogeton zosteriformis
Ranunculus trichophyllus

of the joint-occurrence group to which each species belonged was used to weight the species' relative frequency in each stand. The products of relative frequency and joint-occurrence number for each species were summed to provide a compositional index for each stand.

Forty-one stands, chosen by uniform criteria and sampled by comparable methods were arranged in the numerical order of their compositional indices which ranged from 100 to 400. The relative frequencies of each species in all stands were plotted on a graph against the index (Figure 4). The sums of the relative frequencies of all the species in each of the four joint occurrence groups were also plotted against the indices and produced similar discrete curves. At first sight, it might appear to those unaccustomed to working with weighted index values that the plotting of relative frequencies against a product including relative frequency as a component is a meaningless manipulation. Upon consideration, however, it can be seen that the situation is not comparable to plotting values of A against values of A x W. The summation nature of the index means that values of A are being plotted against (A x W) + (B x W) + (C x W) + ... (N x W). In this circumstance, the actual magnitude of A has

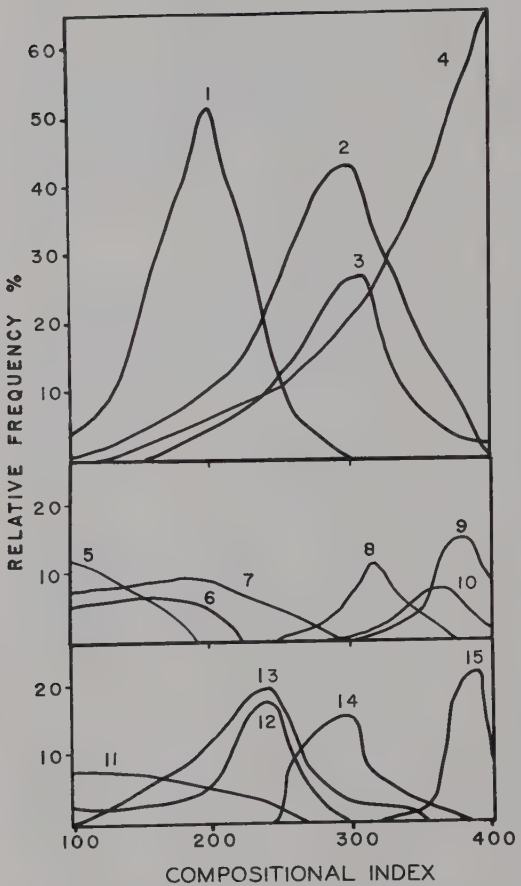

FIG. 4. Relative frequency (smoothed curves) of important taxa plotted against the compositional index. Taxa: 1. *Isoetes* spp., 2. *Najas flexilis*, 3. *Vallisneria americana*, 4. *Chara* spp., 5. *Elatine minima*, 6. *Potamogeton epihydrus*, 7. *Myriophyllum tenellum*, 8. *Heteranthera dubia*, 9. *P. illinoensis*, 10. *P. zosteriformis*, 11. *Juncus pelocarpus* f. *submersus*, 12. *Eleocharis acicularis*, 13. *P. gramineus*, 14. *Anacharis* spp., 15. *M. exalbescens*.

very little influence in determining the value of the index and is essentially an independent variable. This can be easily checked by using a random numbers table to supply values for hypothetical species in randomly mixed communities. When this is done and the entire procedure carried out, each species gives an irregularly straight line when plotted against the index, instead of a group of non-identical but overlapping curves as in Figure 4.

When the relative frequency curves for all species were superposed, the graph in Figure 5 was the result. It illustrates that when the stands studied were arranged in an order based upon the association tendencies of their constituent species, the relative frequencies of the species form curves which overlap and whose peaks are distributed throughout the array. The overlapping of curves and lack of clearly discrete groups justifies the designation of these communities as a vegetational continuum.

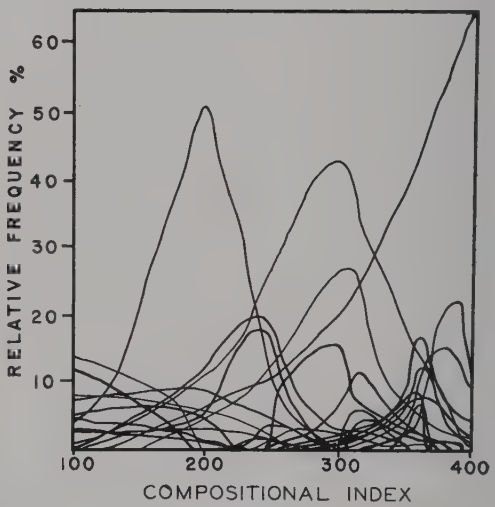

FIG. 5. Relative frequency (smoothed curves) of taxa plotted against the compositional index.

The change in physiognomy of the species is also a gradual one, ranging from small plants, often of a rosette type, in the low index stands to large shrub-like plants in the higher index stands. The chief exception is *Chara*, some species of which, although small in stature, form dense beds in the very high index stands. The vegetation of four hypothetical stands typical of those at indices of 100, 200, 300, and 400 are diagrammed in Figure 6 to illustrate the proportion of species of each type in each stand. The arrangement of species on the diagram is unrelated to their spatial arrangement in the stands.

ENVIRONMENTAL CORRELATIONS

The most important chemical factors which influence submerged plants are probably the water which surrounds them and the substrate in which they are rooted. Submerged plants obtain gases necessary for photosynthesis and respiration from the water, and those which are rooted obtain most of their nutrients from the substrate, as well as being anchored by it (Pond 1905; Snell 1908). Although agitation by movement of water, and pressure exerted by depth may have a physio-

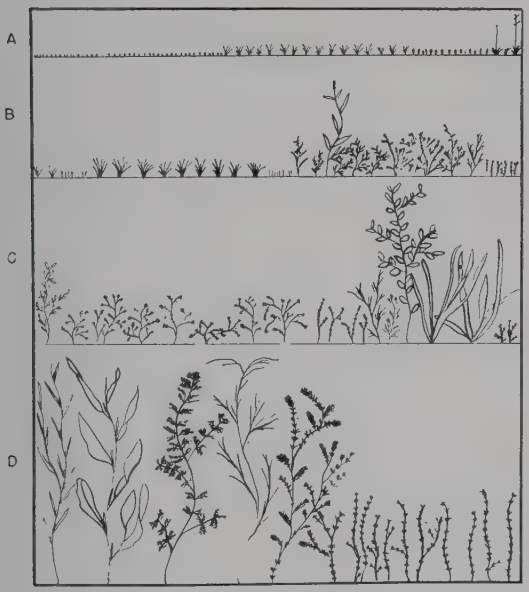

FIG. 6. Diagrammatic illustration of physiognomy along the gradient in representative stands at indices of 100 (A), 200 (B), 300 (C), and 400 (D). The proportion of horizontal space occupied by each species represents its relative frequency in the community. No attempt was made to portray the actual spatial arrangement of species within each stand.

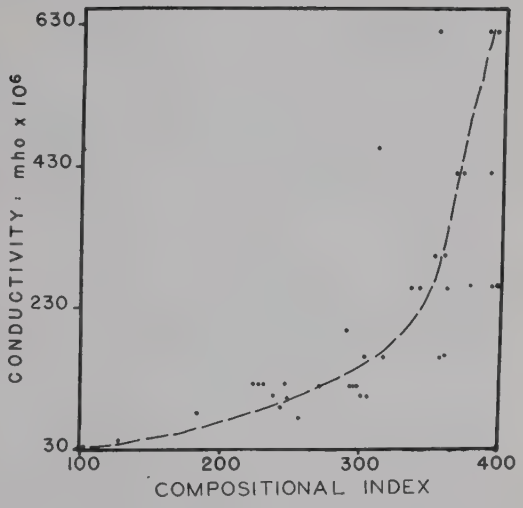

FIG. 7. Conductivity of the water in relation to the compositional index. The dots represent stands for which conductivity measurements were obtained.

logical influence on submerged plants (Kahl 1951, Gessner 1952), these factors are probably negligible within the limits of this investigation. It is probable that moderate depth and water movement exert most of their influence by their effect on the nature of the substrate. Fluctuation of water levels, which may be a very important physical factor in certain areas and types of lakes or ponds, is of little consequence to the lakes in this study.

Of the environmental factors measured, the conductivity of the water is the one which was most smoothly correlated with the vegetational continuum. The conductivity ranged from 30 mho x 10^6 in a stand with an index of 100 to 621 mho x 10^6 in a stand with an index of 394. There was a steady increase in conductivity along the phytosociological gradient, which is illustrated in Figure 7. That the qualities of the water cannot be solely responsible for the character of the plant communities growing in it, however, is indicated by some of the irregularities in the correlation. Stronger evidence might be educed from the fact that communities with varying indices are very often found in the same lake, as was demonstrated with data from Ellen Lake. This situation can be found in almost any lake which has an open, sandy-bottomed or gravelly shore and a sheltered bay. The bays usually contain species whose frequencies peak higher on the gradient than do those of the sandy-substrate areas. Wilson (1935) noted that in some Vilas County lakes rosette-type species were found on exposed, sandy-substrates, and species of the long, flexuous stem and leaf type in the bays with richer substrate.

The influence of substrate may also be noted in data from Lake Ripley. The vegetation of stands at five depths in a single community area was correlated with the substrates in those stands. With depths increasing from 6 inches to 5 feet, the stands had index values, respectively, of 317, 356, 370, 362, and 393. The relative frequencies of the individual species likewise showed regression with depth. Presumably, since wave action kept the water in circulation, the water qualities were similar in all stands in that one area, and the changes in plant communities were related to changes in substrate. The correlation of species with substrate which was noted in this investigation is supported by the more extensive data of Pearsall (1920), Rickett (1922, 1924) and others.

Since certain soil qualities are correlated with individual species and with stands within single lakes, it is of interest to note that correlations with the whole phytosociological gradient also exist. The substrates of the stands with high indices contained more marl and organic matter and less sand than did those with low indices. The sand content of the substrate decreased with rise in index. The calcium carbonate content of the substrate increased somewhat irregularly from a trace in the

stands of lowest index to 95% in a stand with an index of 393. The soil organic matter also increased, but more irregularly, from a trace in stands at 100 to 66% in a stand at 400. Soil reaction ranged from pH 5.4 in low index stands to pH 8.0 in high index stands. Soil calcium, magnesium, and nitrate were positively correlated with the index values while phosphorous, potassium, and ammonia fluctuated irregularly.

The interplay of water and substrate as compensating factor complexes which influence the species combinations in any given stand suggest that meaningful representation of species behavior could be made on two dimensional graphs, with water composition on one axis and soil composition on the other. The number of stands available in this study was too small to provide an adequate coverage of all combinations of such factors and hence such graphs are not presented. Tentative use of this technique, however, indicated that species which were similar with respect to their correlations with water conductivity were sometimes very different with respect to substrate condition. One example was *Chara,* which was most abundant in water of high conductivity, but which was largely restricted to sites with a marl bottom within this conductivity range. Unfortunately, in this case, interpretations are confused by the fact that *Chara* is the most active agent in the production of marl, and the observed relation may as easily be an effect as a cause.

Summary

An ecological investigation of the communities of large, submerged aquatic plants in Wisconsin lakes was carried out during the summers of 1952 and 1953, with emphasis on the vegetation of eutrophic lakes.

Stands were limited by homogeneity requirements to the vegetation at single depths within uniform areas of lakes. Each stand was sampled by 20 quadrats, 300 sq. in. in area.

Indices were calculated from the joint occurrence of species within the quadrats and were used to derive an order of species related to the gradient complex of ecological factors. The order of species thus derived was used to weight the relative frequencies of the species in each stand. The weighted relative frequencies of the constituent species were summed for each stand, thus giving an index by which the stands might be arranged in order. When the stands were arranged according to these values and the frequencies of the species plotted against the resulting gradient, a pattern of continual change of community composition resulted which was similar to that designated in other studies as a vegetational continuum.

The submerged communities often vary considerably in different parts of the same lake, those in bays and sheltered places with rich soils having communities with higher index values than the equivalent communities on the exposed shores with poorer soils. Likewise, in a single area, the communities usually vary with depth and there are positive correlations between the position of the stands on the phytosociological gradient and the substrate at the various depths.

The majority of the plants in the stands with low indices are small, often rosette-form plants. Those in the high index stands tend to be plants of large stature and/or bulk. There is a continuum of plant physiognomy as well as a continuum of species in the Wisconsin lakes.

With a few exceptions these generalizations can be made: Stands with high indices have distinctly higher water conductivities, organic matter, marl, calcium, magnesium, and nitrate content, pH, and have less sand in their substrates than the stands in the lower part of the gradient. There is evidence that the various factors interact with and compensate for each other in influencing the nature of the plant communities.

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DEW AS AN ECOLOGICAL FACTOR
I. A REVIEW OF THE LITERATURE[1]

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INTRODUCTION

The role of dew in the water economy of the plant and the subsequent effect on plant distribution has been a subject of study for at least 250 years. During this period four pertinent questions have been asked, some many times, and studies undertaken to answer them. In brief these four questions are: (1) What is the distribution of dew? (2) What is the specific physiological response of the plant to dew? (3) Where does the presence or absence of dew directly or indirectly permit or prevent the growth and survival of a particular plant? (4) Where does the presence of dew affect the relative capacity of two or more species to occupy a particular area?

Considerable data pertaining to the first three questions can be found in the literature, but little can be found pertaining to the fourth. This is not surprising since the more obvious and more readily measurable relationships are generally studied first. However, judging by the data presented in the literature it appears, at this time, that dew is not of particular importance in controlling the general distribution of plants. Therefore studies pertaining to the effect of dew on the relative capacity of two different species to occupy a particular area assumes major importance.

The studies presented in this series of papers are concerned with this fourth question. The initial phases deal with the specific response of different species to dew when subject to high moisture stress, i.e. soil at the permanent wilting point. Studies to date have been conducted in the greenhouse and have not yet justified complementary studies in the field.

This paper is confined to a résumé of the more pertinent literature on the subject of dew. Not every published report relating to the subject has been included. For example there are a number of papers concerned with the amount of water added directly to the soil by dew as well as the amount of water that is condensed within the soil itself; and there are a number of papers reporting on the relationship between dew and the incidence of certain plant diseases, that have not been included. The specific purpose of the literature review as presented here is to give the reader a background so that he will be in a better position to appraise the results of the greenhouse studies that will be presented in succeeding papers.

LITERATUE REVIEW

The work by Hales (1727) is the first published account on dew and its utilization by the plant. He demonstrated, to his own satisfaction at least, that plants could absorb dew and rain through their leaf surfaces. However, when one examines his techniques there is some question as to whether or not absorption of moisture by the clay pots themselves might have been responsible for the observed change in weight.

The implications of these data were either inadvertently or purposely overlooked by the plant physiologists during the next hundred years (De

[1] Work carried out as part of University of Calif. Agric. Exper. Station Research Project 1577.

Candolle 1832, Meyen 1837) and it was not until the experiments of Duchartre (1857) that the subject of dew absorption was again seriously considered.

Being already convinced that dew and rain were absorbed through the leaf, Duchartre (1857) set up experiments to demonstrate the phenomenon. However, the experimental data did not support his original assumption and he was finally forced to conclude that water was not absorbed, to any appreciable extent, through the leaves.

Approximately twenty years later Boussingault (1878) in France and Henslow (1880) in England independently restudied the question and both came to the conclusion that dew and rain could be absorbed and utilized under certain circumstances to supplement the water supplied by the roots. Henslow in particular felt that there was no longer any room for doubt and stated ". . . the subject of this paper has been a matter of controversy for 150 years; but it is hoped that at last the question whether moisture of any kind is absorbed or not by the aerial parts of plants will be set at rest forever and answered in the affirmative."

Accordingly, Schimper (1884) supported the concept that dew could be absorbed in the green tissues of the plant with data he had collected on the behavior of epiphytes in the tropics; while Volkens (1887) supported it with data collected relative to plants living in the Egyptian-Arabian desert. However, this unanimity of opinion soon came to an end with the publication data by Ganong (1894) indicating that when plants of *Helianthus, Pelargonium, Begonia, Coleus, Senecio,* and *Ricinus* were grown in sealed containers until they had wilted they could not absorb moisture through their leaves.

Of the early studies on water absorption by the aerial parts of the plant, one of the most definitive was carried out by Lloyd (1905) at the Desert Botanical Laboratory in Tucson. He was able to show by a simple wick arrangement that the desert shrub *Fouquieria splendens* could utilize water absorbed through the stem or bud scales for active leaf growth. During the summer this shrub normally loses its leaves but is peculiar in being able to send out new ones in a few days after water has been made available to its roots. When Lloyd intermittently wetted the upper part of the stem of one of these shrubs by wrapping it in cotton gauze, the end of which dipped into a reservoir of water, new leaves soon developed on that portion of the stem, thus indicating that the water was absorbed.

The year following this study Cannon (1906) noted that many plants of this same species had kept their leaves well into the hot summer weather and ascribed this to the unusually high humidities prevalent at the time, which he assumed reduced the transpirational loss. However, in addition he suggested that ". . . leaves of the plants might really absorb atmospheric moisture in sufficient amounts so as to be of biological importance."

Spaulding (1906a, 1906b) also at the Desert Laboratory investigated the uptake of water in both the liquid and vapor phase by leaves and stems. He found the leaves and/or stems of some desert shrubs absorbed water in both the liquid and vapor phase while those of others did not. However, he concluded that even when absorption by the leaves and/or stem occurred it was so slow that ". . . the roots of desert plants constitute their only reliably active agent in providing a normal water supply."

Drable and Drable (1907) in England measured the osmotic concentration of the cell sap from leaves of several plants. They also placed isolated leaves from some of these plants in water and noted that it was readily absorbed. These two general observations suggested to them that a high osmotic pressure in the leaf cell might enable the plant to absorb water from the atmosphere. Then they compared the smooth leaf of the dandelion in the garden to the rough hairy leaf of the dandelion in the dry sand hills and concluded that the hairy surface might be useful by trapping and holding more water on the leaf surface.

In the experiments conducted by Spaulding (1906a) several cacti were included. Apparently their succulent stems were able to absorb water in either the liquid or vapor phase. The amount, however, was so meager it was not considered to be significant. In general this point of view was confirmed by data on some South African succulents submitted by Schönland (1909). He reported that *Crassula cymosa* absorbed water through its succulent leaves and stems, but to only a limited extent while *Mesembrianthemum barbatum* and *Anacampseros filamentosa* did not absorb any appreciable quantity. However, Marloth (1909) did not agree with this conclusion and after a detailed study on the apical hairs on the succulent leaves of *M. densum* and *M. barbatum* reported that these hairs were admirably adapted to the absorption of water. Later Marloth (1926) reported that the hair structure on several species in the Liliaceae and Amaryllidaceae also appeared to be adapted for water absorption and proceeded to demonstrate such absorption with at least three of the species.

Salicornia ramosissima, another succulent, but from the salt marshes, was also studied (Halket 1911). Apparently it too could absorb water through its aerial parts, but the amount absorbed was only a small fraction of the water taken up by the roots. No additional studies were carried out and the ecological value of such water absorption continued to be a matter of speculation.

Although the efficacy of dew had not been established, both Sigmond (1912) and Wagner (1912) assumed it was important to the growth of the forest tree. Their studies indicated that the northwestern and northern borders of the forest stand were the most advantageous for dew formation and moisture in general. Wagner even went so far as to develop a forest cutting system based upon this relationship. Whether or not dew per se plays an important role in this system is difficult to determine. Certainly the presence of lowered moisture stresses would be expected on such north borders even in the absence of dew. At any rate, the concept has continued to be accepted over the years. For example Pfeffer, et al. (1948) stated ". . . in preparing to cut in a forest stand one can best benefit the remaining young growth with regards to supplying them with dew if one orientates the cutting in such a manner so that the remaining trees will shade the dew covered areas."

The study by Gates (1914) is of particular interest. He carried on a series of water balance measurements with several evergreen shrubs and trees in Michigan. During the winter he found that a severed branch took up moisture on a frosty night equal to three or four times the amount lost by transpiration from the same branch on a cold winter day. He was thus able to suggest how evergreen shrubs and trees could maintain a satisfactory water balance in spite of a frozen soil and a continued daily transpirational loss.

Twenty years later Michaelis (1934) and Michaelis and Michaelis (1934), in a more elaborate investigation carried on close to timberline in the Swiss Alps, came to the same conclusion. In brief, they followed the water balance in spruce branches that were cut in December and suspended under the shade of the crowns until March. When the loss in weight of these branches was found to be less than would be expected from the transpiration measurements, they concluded that part of the transpirational loss must have been replenished by dew that formed at night.

Still more recently Rouschal (1938, 1939) has presented data on some common garden evergreen plants. Apparently dew absorbed during the night by these plants balances the small transpirational loss that occurs during a winter day.

Wetzel (1924) investigated the water absorbing ability of leaves from over 100 species native to the temperate region. Most of the leaves were able to absorb water, and the cuticle, however, strongly developed, was generally not an insuperable barrier to the passage of water. Only when the leaf possessed a waxy bloom or a thick covering of hairs was water absorption prevented. He also studied a series of plants, including some xerophytes normally restricted to rock outcrops, in their natural habitat. He compared the daily loss of water with the amount the plants were able to absorb when their leaves were moistened with dew or artificially sprinkled with water. Even in wilting plants dew did not supply more than 5-10% of the daily expenditure of water. Wetzel concluded that in the Central European plants he investigated, absorption by the aerial organs is not important in supplying water to the plant, and such absorption cannot even begin to replace the absorption of water through the root system.

Wood (1925) in Australia compared water absorption by branches cut from *Eucalyptus corynocalyx, Sterculia diversifolia, Acacia decussata,* and *Atriplex vesicarium.* Since he felt that sprayed moisture might be retained in the capillary spaces between the vesicles or hairs which cover the epidermis and thus cause an apparent absorption, the amount of water absorbed was determined by measuring the increase in weight of the branch when placed in an atmosphere nearly saturated with water vapor. He found no absorption by the cutinized leaves of *Eucalyptus corynocalyx, Sterculia diversifolia,* and *Acacia decussata,* but there was a considerable absorption by the uncutinized leaves of *Atriplex vesicarium.* Wood (1925) suggested that this rapid absorption might be due to the high salt concentration of its tissue and the resulting osmotic concentration of the cell sap. Again, unfortunately, there was no follow-up with studies on the ecological value of potential dew absorption by the salt bushes.

Hiltner (1930, 1932), Zattler (1932), Arens (1934), and Lausberg (1935) were all concerned with the fact that dew, unlike water taken up by the roots, was free of salts. Hiltner (1930) presented extensive data on the yield of mustard and oats grown in pots with different amounts of fertilizer, in both the presence and absence of artificial dew. In the presence of dew he reported increased yields and suggested this was due to the dilution of the cell sap which thereby ". . . equal-

ized the salt concentration which had become too high through normal root absorption."

Zattler performed similar experiments with hop and hemp which were more sensitive to salt than mustard and oats. He found that the effect of spraying the plants (artificial dew) depended upon the amount of fertilizer the plants received; the effect of dew could either increase or decrease the yield.

Arens and Lausberg were of the opinion that the effect of dew results from the leaching of salts from the leaves.

Polansky (1931) concluded that the seedlings of different species of trees differed in the extent to which they were able to utilize dew. *Picea excelsa* seedlings, for example, appeared better able to utilize dew than *Pinus silvestris* seedlings. Since he did not present any quantitative data nor seal off the ground surface during the study, his conclusions cannot be taken very seriously.

Phillip (1932) and Stocker (1933) concluded that dew had a potentially harmful effect because it moistens the cell walls thereby increasing their infiltration capacity and decreasing their resistance to evaporation. This they felt could cause a slight temporary increase in transpiration.

Leick (1933) discussed, at considerable length, methods of measurement and presented some very general data. The data, however, were not convincing and did not support his conclusion, namely that dew was effective through its reduction of the transpirational loss.

Krause (1935) carried out a study of absorption of water by the leaves of a number of species, partly in the field and partly in the laboratory. She found that the rapidity of water absorption by wilted leaves was highly variable and on the basis of this characteristic distinguished three groups. The group with rapid absorption consisted mostly of mesophytes, but some xerophytes were included; the group with moderate absorption consisted mostly of leafy trees, although again some xerophytes were included; the group with very slow absorption consisted of plants with leathery leaves, orchids, succulents and some of the ferns. In general the resistance against absorption appeared to be proportional to the resistance against cuticular transpiration.

Walter (1936) carried out extensive observations in the Namib fog desert of South West Africa. He concluded that absorption of dew and fog by the aerial parts of the plant was unimportant. However, qualitative data were lacking. Fifteen years later Walter (1951) wrote ". . . we cannot attribute to the direct absorption of dew any essential role in supplying the water of the plants . . . a much greater importance for dew and fog is that of the reduction of transpiration and is possible wherever dew is falling and remains in the morning for a long time . . . the distinct decrease of water shortage in plants covered with dew is mostly due to the water absorption of the roots with the completely restricted transpiration of the shoots . . . dew can be of importance in an ecological sense when often a slight decrease of transpiration is decisive for the plant."

Pisek and Cartellieri (1939) presented some interesting data and calculations on the decrease in transpiration of plants covered with dew in the mornings of dry days. From their data it would certainly appear that under some conditions this effect of dew could be very important.

Lehmann and Schanderl (1942) using the Kessler-Fenssicher dew recorder concluded that a morning measurement of the quantity of dew does not correspond to the quantity really precipitated during the night. They also examined some plant hairs and concluded as Volkens (1887) had earlier, rightly or wrongly, that these hairs collected dew, some of which was absorbed by the living basal cells of the hairs. They speculated about the role of such hairs in the water relations of the plant especially in the dry season.

Wahlin (1943) worked with the ferns *Polypodium* and *Phyllitis* and found that they could absorb through their leaves both liquid water and water vapor. Later Potts and Penfound (1948) reported that *Polypodium polypodioides* required liquid water for its development, but nevertheless was also able to absorb water vapor. They also reported that this ability to absorb water vapor persisted even when the surrounding air was not saturated with moisture.

Stålfelt (1944) in a thorough study, measured transpirational loss by needles of *Picea excelsa,* as well as water absorbed by the needles. He found that the transpiration rate of trees on dry sites was less than for those on more moist sites (1.9 kg. per sq. m. per day and 3.4 kg. per sq. m. per day respectively). He also found that as much as 33% of the transpirational loss, during periods of drought, can be reabsorbed by the needles from rain or other moisture falling on the tree; dew absorption he considered to be of only minor importance in this regard.

Steubing (1949) used the fluorescent characteristics of berberine sulfate to follow the absorption of dew by leaves of both xerophytes and mesophytes. Although absorption by the xerophyte was slower he was still able to show in their

leaves an inverse movement of dew all the way back into the vessels.

Stone, et al. (1950) demonstrated that *Pinus coulteri* seedlings could remove an appreciable amount of water vapor from the air, once the relative humidity reached ninety percent or higher, provided a high moisture stress had been previously developed in the seedling. To create this stress they gradually reduced the moisture in the surrounding soil to the permanent wilting point (of the sunflower) and then subjected the needles to a dry blast of air for the 24 hour period immediately prior to the tests.

Arvidson (1951) conducted extensive field measurements on the Isle of Oland in southeastern Sweden where summer drought conditions often develop. Here, he concluded, many shrubs and trees, such as ash, oak, and poplar apparently utilize atmospheric moisture by absorbing it through the leaves. Rain, dew, and fog all appeared to be important sources of moisture. General observations (rather than specific measurements) suggested that in late summer the nocturnal uptake of dew may exceed the daily transpiration loss even in the absence of soil drought.

General field observations in Natal suggested to Meidner (1954) that several of the native species regularly subjected to severe soil moisture deficiencies were able to absorb water from dew deposited on their leaves. One of these species *Chaetacme aristata* was selected for study because dew seemed to disappear more rapidly from its leaves than from the leaves of associated species. Water in-flow was observed by using selective vital stains, and quantitative results were obtained by timing the disappearance of small known volumes of distilled water from the surface of leaves kept in a water saturated atmosphere. However, because it is difficult to maintain a saturated atmosphere and at the same time eliminate temperature gradients which induce evaporation in an apparently saturated atmosphere, Meidner's data must be viewed with some reserve.

One special aspect of dew absorption and its utilization by the plant is the process of water redistribution within the plant itself. The reports by Magistad and J. F. Breazeale (1929), J. F. Breazeale (1930), and J. F. Breazeale and Crider (1934), present some of the first work on this water redistribution problem. Their work indicated that the roots of both corn and tomato plants could absorb water from soil above the wilting point and then "pump" it out again through other roots as they grew into soil which was below the wilting point. Hendrickson and Veihmeyer (1931) questioned these results when they were unable to observe this phenomenon with sunflower and beans.

A few years later Wadsworth (1933) carried out a series of experiments with sugar cane which supported Breazeale's conclusions regarding the outward movement of water through the roots into the soil. He found that either light rain or spray from a garden hose falling upon the leaves of a potted sugar cane plant increased the moisture content of the soil surrounding the roots. Since the soil surface was sealed off by an asphalt emulsion, he concluded that the increased moisture content of the soil was the result of water moving back through the leaves into the plant and then out through the roots into the soil.

Brierley (1936) did not observe any build-up in soil moisture when wilted raspberry plants were exposed to a water spray, but he did note that when one of a pair of joined wilted canes was sprayed the leaves on both canes became turgid again. This meant that the water applied to the wilted leaves of one cane must have moved in and downward and then upward into the other cane.

Recently E. L. Breazeale et al. (1950, 1951a, 1951b) and E. L. Breazeale and McGeorge (1953) reopened the question of the redistribution in the plant of water, such as dew, falling on the leaf surface. They reported that both tomato and corn plants could move water back into the soil. In addition they found soil was not necessary. Water could still be "pumped" back out through the roots even when they were sealed into an empty flask.

Haines (1952, 1953) enlarged upon the empty flask experiment and obtained a similar accumulation of water in the flask with either a tomato plant or a cotton wick. When, however, the temperature of the flask was held constant, water failed to accumulate.

Hohn (1951) unlike Haines was unable to repeat any of Breazeale's results. However, he did find that liquid water is more easily absorbed than water vapor by the shoot part of the plant. He also demonstrated that water could be evaporated from an object even though the surrounding atmosphere was apparently saturated with water.

Janes (1954) in agreement with Hohn, found that plants could continue to lose water through their leaves even in a continuous fog-spray.

Stone and Fowells (1955) reported that seedlings of *Pinus ponderosa* could reduce the soil moisture below the ultimate wilting point of the sunflower and that under this high moisture stress, artificial dew at night prolonged the life

of the seedlings as much as a month and a half. It was not apparent from their data how this was accomplished.

In an effort to elucidate the mechanism involved, Stone et al. (1956) studied the intake of water through the needles of *P. ponderosa* seedlings from a continuous mist spray and its subsequent redistribution. This was with seedlings rooted in soil and with seedlings whose roots were sealed into empty flasks. They found that water moved back through the plant and out through the roots into the empty flasks only when the temperature in the flasks was allowed to fluctuate and there was a concomitant drop in the relative humidity of the air surrounding the roots in the flask. Those plants whose roots had been sealed in soil failed to show any backward movement of water out through their roots. Therefore, they concluded that the prolonged survival of pine seedlings in soil at the wilting point, when the tops receive dew at night, is due to a resaturation of the needle tissue and concomitant reduction in the amount of moisture removed from the root system.

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DEW AS AN ECOLOGICAL FACTOR
II. THE EFFECT OF ARTIFICIAL DEW ON THE SURVIVAL OF *PINUS PONDEROSA* AND ASSOCIATED SPECIES[1]

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Pinus ponderosa is widely distributed throughout the mountainous area of western North America. To the east it extends into the Dakotas and Nebraska; to the north it follows the Rocky Mountains on into southern British Columbia; and to the south it runs along the mountain tops into Baja California and Mexico proper.

In California it is found throughout the mountains of the State. At middle and lower elevation in the Sierra and inner north coast ranges it has a continuous distribution, while in the middle and south coast ranges it is found only in a few scattered locations.

Throughout its range the associated species change. For example, in the coastal mountains near Santa Cruz, California, where precipitation may exceed 100 inches per year, it grows in a few scattered stands in association with *Sequoia sempervirens*. On the other hand, in the northeastern part of the State, near Susanville, where precipitation rarely exceed 20 inches per year, it grows in association with *Juniperus occidentalis, Artemisia tridentata,* and other xeric species. However, over its entire range *P. ponderosa* is exposed to long periods of drought. Even in the coastal mountains where it grows in association with *Sequoia sempervirens* it is largely restricted to sandy soils which retain only a small percent of the heavy rainfall received during the winter.

In the arid northeastern part of the state, stands of *P. ponderosa* often become locked or stagnated at an early age. Clumps of trees 6-10 feet high and 2-4 inches in diameter may average 50-75 years of age. This is in sharp contrast to areas immediately to the west where precipitation is 30-40 inches per year. With increased soil moisture individual trees assert their dominance at an early age and young stands do not stagnate; fifty year old trees are 50-75 feet high and 15-30 inches in diameter.

Again in the arid area, mature stands of *P. ponderosa* are relatively open with as much as 60 percent of the full light intensity reaching the forest floor. Even so, the young trees in the scattered understory are badly suppressed. However, once the mature trees are removed these suppressed trees resume growth. Apparently, this is not because of the increased light intensity, but is because more moisture is made available to the roots of the remaining trees.

Thus it would appear that in this dry northeastern part of California water is so nearly limiting that it must play a critical role in the kind of species association that develops. If this is true, there should be a correlation between the relative capacity of the individuals of the different species to occupy a particular piece of ground and one or more specific physiological characteristics associated with the water economy of the individual plants.

Pertinent data have already been published on the drought resistance of *P. ponderosa*. For example, Fowells and Kirk (1945) found seedlings of this species had the capacity to remove water from soil already at or below the permanent wilting point of the sunflower. Later, Stone and Fowells (1955) found that under greenhouse conditions the length of time that seedlings of *P. pondersoa* could live in soil reduced to the permanent wilting point was increased up to a month and a half by the presence of artificial dew at night. From their data it appears that the seedlings of *P. ponderosa* have certain genetically fixed physiological characteristics that permit them to exist in soil after it has reached the permanent wilting point of the sunflower, provided there is abundant nightly dew fall.

One should not, however, conclude at this point of study that such a physiological characteristic is an important factor in the capacity of this species to invade, occupy, or dominate a particular piece of ground. First it is necessary to determine to what extent associated species also have the capacity to withstand soil drought and to utilize dew. Then it will be necessary to determine the distribution and amount of dew that occurs in the area.

The data presented in this paper are from studies conducted in the greenhouse with seedlings of *P. ponderosa* and three other species that are associated with it in northeastern California, namely, *P. jeffreyi, Abies concolor,* and *Libocedrus decurrens*. Both the effect of abundant nightly artificial dew and the capacity of the seedlings of these species to continue to live in soil

[1] Work carried out as part of University of Calif. Agric. Exper. Station Research Project 1577.

after the permanent wilting point of the sunflower had been reached were evaluated.

Method of Study

Although this report includes the results of several different experiments carried on over a three year period, the procedure was generally the same. Two year old (1-1) bare root stock was used. Seedlings of *P. jeffreyi* and *P. ponderosa* were obtained from the U. S. Forest Service nurseries at Oakdale and McCloud; seedlings of *Abies concolor* and *Libocedrus decurrens* were obtained from the California Forest and Range Experiment Station's experimental nursery at Pinecrest. Upon receipt of the seedlings in Berkeley, they were root pruned to approximately four inches and then planted in gallon cans filled with selected soil. Root pruning was necessary to insure the lower half of the soil mass in the cans would be occupied by new actively growing roots.

Three different soils were used: (1) Oakley sandy loam with moisture equivalent of 3.5% and a permanent wilting point[2] of 2.4%; (2) a Dublin clay with a moisture equivalent of 20.5% and a permanent wilting point of 8.7%; and (3) a Sheridan clay loam with a moisture equivalent of 13.5% and a permanent wilting point of 6.9%.

After the seedlings were well established, the moisture content of the soil in each can was reduced to the desired level, either by discontinuing the watering or by first establishing considerable additional transpirational area in each can before the watering was discontinued. This additional transpirational area was provided by growing sunflower plants directly from seed planted in the cans with the coniferous seedlings (Fig. 1). It was necessary to start the sunflowers within three months after the tree seedlings were planted. Otherwise the roots of the tree seedlings physically occupied most of the lower three inches of the soil-mass thus restricting the roots of the sunflower plants almost entirely to the upper three inch layer. The sunflowers were allowed to grow at least twelve fully expanded leaves before watering was discontinued. When this procedure was followed the root systems of the sunflowers were found freely interspersed throughout the entire soil mass (Fig. 1). Consequently the moisture content could be more or less evenly reduced to the permanent wilting point once watering had been discontinued. In the later studies, where the seedlings were allowed to grow for a year or more in gallon cans before being used, it was necessary to reprune the roots and replant the seedlings before they were used.

[2] The permanent wilting point was determined with the sunflower as the test plant.

Fig. 1. Can cut away to show distribution of roots. The dark roots which do not show well are pine roots while the light-colored roots belong to the sunflower plants.

After the moisture content of the soil had been reduced to the permanent wilting point each can was sealed by placing over the top of the can a plastic bag through which the seedling protruded. A water-tight seal around the stem was accomplished with several turns of a fine copper wire and a heavy wrapping of electrical scotch tape (Fig. 2). The bottom edge of the bag was sealed to the can with additional scotch tape and the drain holes plugged with hot paraffin.

All experiments were carried on in the greenhouse where the temperature never dropped below 20°C at night, but occasionally exceeded 40°C during the day. In the winter and spring the evaporative power of the air was considerably less than during the summer and fall. This nec-

FIG. 2. Can covered with plastic envelope after the sunflowers had died and had been clipped off.

essarily ruled out any absolute comparison of survival of the different species when experiments were performed during different times of the year. Consequently, when a comparison of species was desirable, it was necessary to study all the species at once.

To obtain normal growth of the sunflowers in the Oakley and Sheridan soils, it was necessary to water regularly with Hoagland's nutrient solution, increased to five times its regular strength.

The soil moisture percent was calculated on a dry weight basis and was determined from three soil samples taken from each one inch of soil depth. The samples were dried in an oven at 100°C for twenty-four hours and because of the low organic content, the loss in weight could be accurately assigned to the water content of the soil. In a few of the later experiments only the 2-3 inch depth and the 4-5 inch depths were sampled. This was sufficient for the purposes of these particular experiments.

A fine mist spray was provided by using a standard commercial fogging nozzle. The spray was turned on for a twelve hour period each night. However, due to the scheduling problem, some weeks this meant 7:00 P.M. to 7:00 A.M.; other weeks it meant 8:00 P.M. to 8:00 A.M.; and on a few occasions it meant 9:00 P.M. to 9:00 A.M.

Initial experiments indicated that after several weeks of operation, leaks were likely to develop. To minimize this problem, in later studies the cans were turned on their sides and placed in a bladeless guillotine-like structure which prevented any spray from landing upon the plastic bags sealing the cans (Fig. 3). In one experiment a large plastic sheet replaced the hard-board used in the guillotine-like structure. With such an arrangement it was possible to stack one can upon another and save considerable space. Although this last arrangement was adequate it did not completely keep the spray from falling on the individual cans and after five months some water had leaked into the top row of cans. In the experiments reported here the author feels confident that leaks were detected when they occurred and that altered survival under spray was not the result of undetected leaks.

FIG. 3. Canned seedlings in rack ready for exposure to mist spray. Each seedling was sealed in a can with a plastic envelope after the sunflowers, which reduced the soil moisture to the wilting point, had been clipped off.

The reliability of the death-point estimates was checked in each experiment. This was accomplished by removing during the experiment several cans containing plants judged to be dead or judged to be alive. The plastic bags were then removed, water added, and the reaction of the seedlings noted. After a little practice one became adept at this "detection game." For example, out of more than 100 plants so checked not one seedling assumed to be dead revived when water was added; and conversely not one seedling

assumed to be alive died when water was added. However, there is a short period of time when it is impossible to determine by visual means whether the seedling is dead or alive. With *Abies concolor, P. ponderosa,* and *P. jeffreyi,* it is a 2-3 day period and with *Libocedrus decurrens* it is a 4-7 day period.

Throughout this paper the permanent wilting point of the sunflower refers to the soil moisture percent at which the sunflower wilts, but can be revived in a saturated atmosphere; while the ultimate wilting point of the sunflower refers to the soil moisture percent at which the sunflower dies (Furr et al. 1945, Taylor et al. 1934),

In making comparisons where a statistical expression of significance was needed, the standard error of the difference of the means was calculated and the t-test applied.

Experiments and Results

Interrelated effect of soil texture and artificial dew on the survival of Pinus ponderosa *seedlings*

This experiment was one of the first undertaken. Sunflower were not used, as they were later, to reduce the soil moisture to the permanent and ultimate wilting points. Instead the spray treatment was begun arbitrarily, one month after watering of the seedlings in the sandy loam had been discontinued and two months after watering of the seedlings in the clay had been discontinued. Preliminary tests had indicated that there was little reduction in the soil moisture content from then until the seedlings died.

The soils used in this study were Oakley sandy loam and a Dublin clay. Watering was discontinued September 15 on the clay and October 15 on the sandy loam. On November 15, 8 months after the seedlings had been transplanted to the cans, the cans were sealed with plastic bags and exposure to artificial dew began. Although each can contained two seedlings the data presented here refer only to the conditions associated with the death of the second seedling. In the sandy loam the death of the second seedling generally followed in 1 or 2 days after the death of the first seedling; in the clay, death of the second seedling often did not occur for 6 to 10 days after the death of the first seedling.

After the cans were sealed, 120 of them (half with clay and half with sandy loam) were selected on the basis of the uniformity of the seedlings they contained. Ten of the cans with sandy loam and 10 of the cans with clay were selected at random and the soil moisture determined for each 1 inch of depth within each can. Three samples were taken from each one-inch layer of soil as it was dug from the can, and the moisture content per layer expressed as the average of the three samples.

This left 100 cans which were all kept together on the same greenhouse bench during the daytime. Then for 12 hours each night, one-half of each group, 25 cans with clay and 25 cans with sandy loam, were exposed to a mist spray. The other half were placed in a large wooden desiccator containing $Ca\ Cl_2$ and a circulating fan. In this desiccator the relative humidity was maintained at approximately 25% throughout the night.

The weight of each can was determined once each week, principally as a check on leakage under the spray. In each instance where a leak was indicated by an increase in weight, wet spots were also found. During this study it was necessary to discard 7 of the cans because of leakage.

Five cans from each group were used during the course of the study for a check on the reliability of the death-point estimate. Consequently the study ended with survival and soil moisture data for 20 cans with sandy loam and 20 cans with clay which had not received spray at night and 16 cans with sandy loam and 17 cans with clay which had received spray at night.

In both soils, approximately 95% of the roots were found in the bottom 3 inches of the can. In the sandy loam a well developed, much branched root system occupied this portion, while in the clay this was not true. Instead the root systems were poorly developed with the largest part restricted to the outside layer of the soil mass.

The results of this study are summarized in Table I and Fig. 4.

At the time exposure to spray at night was begun, the moisture content of the sandy loam was significantly less than the permanent wilting point of the sunflower, while the moisture content of the clay was significantly higher. From then on there was no significant change in the moisture content of either soil regardless of the treatment.

Since the sandy loam was approximately 1% below the permanent wilting point and the clay was approximately 1% above, at the time the plastic coverings were placed over the cans, one might expect the seedlings in the clay to survive longer than the seedlings in the sandy loam; and when spray at night was absent the seedlings in the clay survived one month longer than the seedlings in the sandy loam. On the other hand the behavior in the presence of spray at night was not expected. Under this treatment the seedlings in the sandy loam survived as long as did the seedlings in the clay. This meant that the spray at night increased the average survival time in

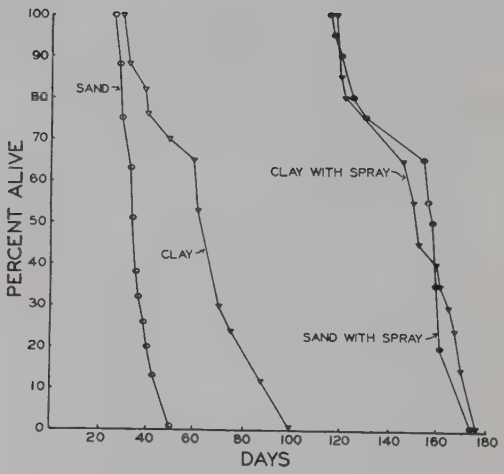

FIG. 4. Survival of *Pinus ponderosa* seedlings on Oakley sandy loam and Dublin clay in the presence and absence of spray at night after cans had been sealed by plastic envelopes.

the sandy loam three months while in the clay it was increased only two months.

Soil moisture removal by Pinus ponderosa *seedlings in the presence and absence of artificial dew*

The general soil moisture pattern that accompanied the prolonged survival of the pine seedlings under spray at night was obtained from the experiment just described (Table I). However, a closer look, with better control of the moisture depletion, was undertaken the following year.

TABLE I. Soil moisture changes after watering was discontinued and subsequent survival of *Pinus ponderosa* seedlings on different textured soils

	Oakley Sandy Loam		Dublin Clay	
	Average	Range	Average	Range
Moisture Percent:				
Permanent wilting point of sunflowers	2.4*	2.2 - 2.6	8.7*	8.4 - 9.5
When cans were sealed	1.4	1.0 - 1.6	10.3	9.2 - 11.0
At death of pine seedling receiving spray at night	1.2	.9 - 1.5	10.2	9.3 - 10.4
At death of pine seedling not receiving spray at night	1.4	1.0 - 1.7	9.9	9.5 - 10.5
Number of days to death of seedling after cans were sealed:				
Seedlings receiving spray at night	152	118 - 174	156	120 - 176
Seedlings not receiving spray at night	36**	29 - 50	63**	33 - 100

*Significantly different (.95 level) from other averages in the same column.
**Survival on clay loam significantly higher (.95 level) than on sandy loam when there was no spray at night.

In April, 3 year old *P. ponderosa* seedlings were removed from gallon cans, in which they had been grown throughout the previous year, their roots trimmed to approximately 3 inches, and the seedlings replanted in gallon cans of Sheridan clay loam. This soil was selected because it had a higher permanent wilting point than the Oakley sandy loam previously used and root penetrability was still good. The higher permanent wilting point meant a larger spread between the permanent wilting point of the sunflower and the ultimate wilting point of the pine seedling. This was important because smaller percentage differences could be detected than would otherwise be possible.

Three months later five sunflower seeds were planted around each pine seedling and when all the sunflowers had developed at least 12 fully expanded leaves, watering was discontinued. When the moisture content of the entire soil mass had been reduced to the permanent wilting point of the sunflower 10 cans were removed and the soil moisture content determined for each inch of depth within each can. Then when the ultimate wilting point of the sunflowers was reached another 10 cans were removed and the soil moisture content again determined for each inch of depth within each can. Then 50 cans were selected, in which the sunflowers had all died within 3 days of each other, the dead sunflowers cut off at the ground level, and the cans sealed with a plastic bag.

These cans were placed together on the same bench in the greenhouse. Then for twelve hours each night one half of the cans were placed under the spray. The remaining 25 cans were not moved and were exposed only to the normal greenhouse humidity which ranged from 20 to 80 percent.

Cans were weighed weekly throughout the study to check for leaks. None however developed.

As the seedlings died the soil moisture content was determined for each inch of depth within each can. The results are summarized in Table II.

Both groups of seedlings—those exposed to spray at night and those not so treated—continued to remove moisture from the soil after the ultimate wilting point of the sunflowers had been reached. Except in the top three inches, the reduction in the soil moisture content throughout the cans, regardless of whether or not they received spray at night, was significant. When the pine seedlings died, the moisture content of the soil surrounding their roots was dependent upon whether or not the seedlings had received spray at night. If they had not, the soil moisture content was significantly lower than if they had.

The root distribution of the pine seedlings ex-

TABLE II. Moisture content of soil (Sheridan clay loam) surrounding the roots of *Pinus ponderosa* seedlings in the presence of artificial dew

Depth in Can	Distribution of the Pine Seedling's Root System	Soil Moisture Content		
		Pine Seedlings Not Sprayed at Night	Pine Seedlings Sprayed at Night	Sunflowers at the Ultimate Wilting Point
Inches	%	%	%	%
0 - 1	trace	2.4	2.9	2.8
1 - 2	trace	4.8	5.2	5.2
2 - 3	5	5.9*	6.3	6.2
3 - 4	20	5.1*	5.6*	6.4*
4 - 5	35	5.2*	5.7*	6.6*
5 - 6	40	5.1*	5.6*	6.5*

*Differs significantly (.95 level) from soil moisture at the same depth in the other two columns.

plains the absence of any significant relationship between treatment and moisture content in the upper three inches of soil. Since there were few pine roots in this zone, the low moisture content was due primarily to water removal, both by sunflower roots that permeated the zone and by direct evaporation from the soil during the interval between the cessation of watering and the death of the sunflowers, at which time the cans were sealed with plastic bags.

Survival of Pinus ponderosa, Pinus jeffreyi, Abies concolor, *and* Libocedrus decurrens *seedlings in the presence and absence of artificial dew at night*

The experimental procedure in this final study did not vary significantly from that of the one just described. The soil was Sheridan clay loam, three year old "repotted" seedlings were used, and the soil moisture was reduced to the ultimate wilting point by sunflowers, before the cans were sealed with plastic bags.

Thirty seedlings of each species or a total of 120 cans were involved. Ten cans of each species were removed when the ultimate wilting point of the sunflowers was reached and the soil moisture determined at the 4-5 inch depth in each can. Then sealed cans of each species were placed upright on a table at one end of the greenhouse. On another table some distance away the other 40 remaining cans, 10 of each species, were set out beneath a fog spray nozzle. These, however, were stacked sideways, one upon another, in two racks and covered with a plastic sheet in which holes were cut to allow the seedlings to protrude. Thus when the spray was turned on at night the tops of the seedling were soon covered with moisture while the sealed cans remained almost dry. This simplified the leakage problem and eliminated the need for weekly weighing.

As the individual seedlings died the cans were removed to the laboratory, the date was recorded and the soil moisture determined for the 4-5 inch depth.

The soil moisture data are summarized in Table III while the survival data are summarized in Table IV and are shown graphically in Figs. 5, 6, and 7.

TABLE III. Moisture content of the soil (Sheridan clay loam) at the death point (ultimate wilting point) of seedlings not receiving spray at night

Species	Moisture Content (4-5 Inch Depth)	
	Average %	Range %
Sunflowers	6.5	6.3 - 7.0
Abies concolor	6.8	5.7 - 7.8
Libocedrus decurrens	6.4	5.7 - 7.3
Pinus ponderosa	6.1	5.2 - 7.3
Pinus jeffreyi	5.3*	5.2 - 5.5

*Significantly different (.95 level) from the other averages.

TABLE IV. Seedlings survival in the presence as well as in the absence of artificial dew[1]

Species	Days Seedlings Survived After the Ultimate Wilting Point of the Sunflower Had Been Reached			
	Without Spray at Night		With Spray at Night	
	Average	Range	Average	Range
Abies concolor	35	20 - 44	55	20 - 76
Libocedrus decurrens	44	35 - 50	116	101 - 130
Pinus ponderosa	64	46 - 87	94	81 - 110
Pinus jeffreyi	95	64 - 120	93	70 - 124

[1]Individual species response to drought within each treatment was significantly different (.95 level) with the exception of *Pinus ponderosa* and *Pinus jeffreyi* under spray at night. Individual species response to spray was significant (.95 level) with the exception of *Pinus jeffreyi*.

Of the four species tested, only *P. jeffreyi* removed a significant amount of water from the soil mass after the sunflowers had permanently wilted and died.

This does not necessarily mean that *P. jeffreyi* is the only species, of those tested, that can remove water after the ultimate wilting point of the sunflower has been reached. With a larger sample *P. ponderosa* seedlings probably would have shown a significant reduction of the soil moisture as would perhaps some of the other species. Actually, with the *P. ponderosa* seedlings the moisture content in only 2 out of the 10 cans were out of line. Had it not been for these two cans the average soil moisture reduction would have been highly significant.

When the seedlings were not exposed to spray

at night, *Abies concolor* died first in an average of 35 days, then *Libocedrus decurrens* in an average of 44 days, then *P. ponderosa* in an average of 65 days, and then *P. jeffreyi* in an average of 95 days.

When the seedlings were exposed to spray at night the picture changed. *Abies concolor* still was the first to die although the spray at night did extend its average survival by 20 days. *P. ponderosa* and *P. jeffreyi* died next at approximately the same time. This, however, meant that the spray exposure was effective on *P. ponderosa* and extended its average survival by 30 days while it was not effective on *P. jeffreyi*. Finally the last to die was *Libocedrus decurrens* whose average survival was extended by 72 days.

Thus, although the length of time the different species were able to survive after the sunflower had died was increased by exposure to spray at night, the exposure was not equally effective in prolonging the survival of the different species.

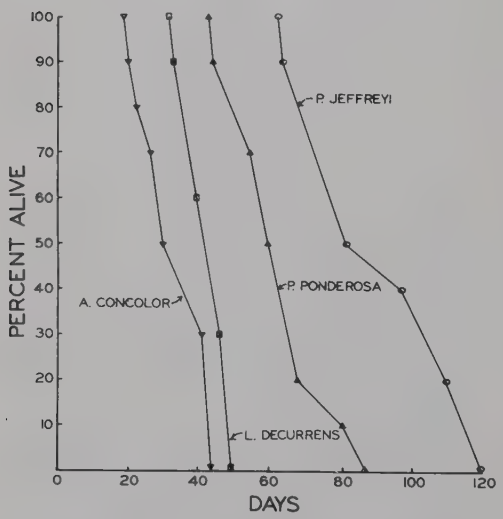

FIG. 5. Survival in the absence of spray at night after the soil moisture had been reduced to the ultimate wilting point of the sunflower.

DISCUSSION AND CONCLUSIONS

The fact that *P. ponderosa* seedlings continued to live in the sandy loam for more than a month after the ultimate wilting point of the sunflower had been reached, is not new (Fowells and Kirk 1945, Stone and Fowells 1955). However, the fact that the pine seedling died in the clay soil even before the permanent wilting point of the sunflower had been reached has not been previously reported. Apparently there is a major

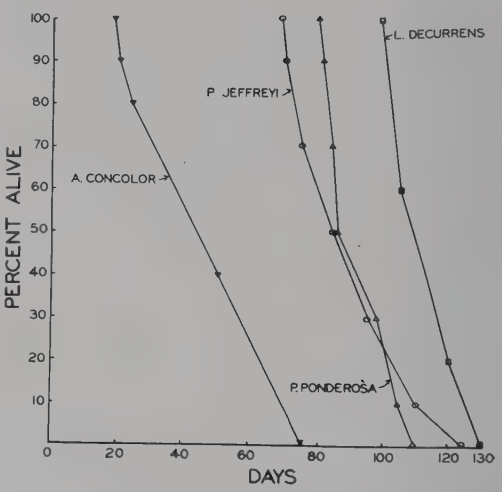

FIG. 6. Survival in the presence of spray at night after the soil moisture had been reduced to the ultimate wilting point of the sunflower.

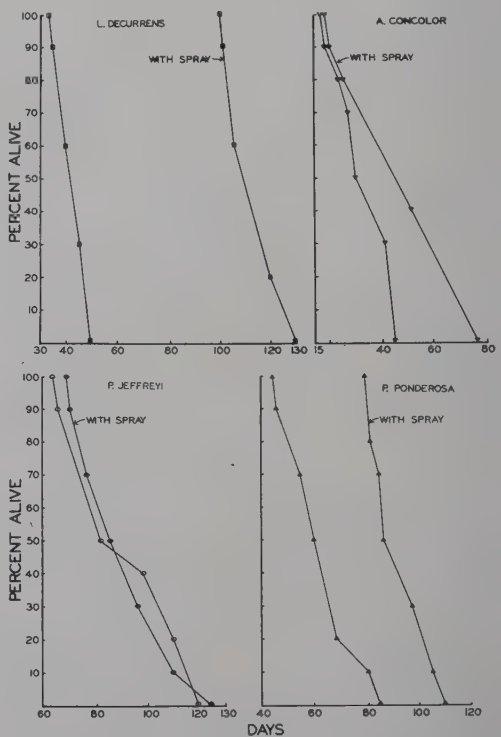

FIG. 7. Survival in the presence and absence of spray at night after the soil moisture had been reduced to the ultimate wilting point of the sunflower.

difference in the capacity of the *P. ponderosa* seedlings to survive extended periods of drought in light and heavy textured soils.

The explanation for this difference would appear to hinge upon the relative degree to which these seedlings develop roots when in soils of different texture. In the clay the root systems were poorly developed with a considerable portion of the soil free of roots, while in the sandy loam the root systems were well developed with scarcely any part of the soil in the lower third of the cans without roots. Probably, in the sandy loam there were enough roots present to remove all of the available water from the soil while in the clay relatively large masses of soil were untapped by roots and as a consequence available water was not removed.

If this general phenomenon occurs under natural field conditions—and there is no apparent reason for believing that it does not—one can easily see how pine could be favored by a light textured soil. As a matter of fact there are some areas where pine occupies only the light textured soils while other vegetation dominates the heavy textured soils. An example of this occurs near Mt. Hermon in the middle coast range of California. There many of the soils have developed from sedimentary parent material and in a few places, where shales and sandstones are interspersed, heavy and light texture soils have developed side by side. In at least one such area, *P. ponderosa* occupies the sandy soil while *Sequoia sempervirens* a few feet away occupies the heavier clay. However, before such a picture can be completed the growth of *Sequoia sempervirens* on light and heavy textured soils must be studied. Until this is done such a suggested relationship must remain speculative.

Artificial dew was effective in prolonging the life of the seedling on both the sandy loam and the clay. This would be expected if its role is, as suggested by Stone et al. (1956), principally one of resaturation of the needle tissue at night and the concomitant reduction in water loss per unit time. At the moment there is no apparent explanation for the greater effectiveness of the spray in prolonging the life of the seedlings on the sandy loam.

The data presented in Table II clearly demonstrate the capacity of the pine seedling to continue water absorption from the soil after the sunflower plants, growing in the same can of soil, had wilted and died. This is not surprising since the initial selection and subsequent general acceptance of the sunflower as a standard plant for determining the permanent wilting point, was based upon its capacity to show physical signs of wilting (Briggs and Shantz 1912). In contrast, the structure of the pine seedling is such that early moisture stress does not show. Even after prolonged stress when the needles, the twigs, and the main stem have shown appreciable shrinkage the pine seedling does not collapse, and with the addition of water the tissues will regain their normal turgidity. Under similar moisture stress the soft leaf tissues of the sunflower collapse and die. When this happens, even though the stem may still regain its turgidity once water is resupplied, the entire plant dies.

Theoretically, the amount of water lost from the soil after the death and subsequent removal of the sunflower is dependent both upon the vapor pressure gradient between the roots of the pine seedling and the air surrounding its exposed top, and upon the length of time the seedling remains alive under these conditions. Thus, a reduction in the soil moisture to its lowest value might be expected from a combination of circumstances which either prolongs the life of the seedling, increases the moisture stress within the plant, or both.

If the data presented in Table II are interpreted this way the life span of the pine seedling was increased by spray at night which reduced the moisture stress within the plant, and which, in turn, reduced the vapor pressure gradient between the seedling and the surrounding air. The combined effect then apparently still allowed some reduction in soil moisture, but not as much as when the spray was withheld. Consequently, when the seedling did not receive spray at night the moisture stress in the seedling was greater, although the period of time the plant remained alive was shorter.

The differential ability of the canned seedling to survive after the sunflowers had wilted and died indicated a basic physiological difference in the drought resistance of *Abies concolor, Libocedrus decurrens, P. ponderosa* and *P. jeffreyi*. The experimental evidence indicated that *Abies concolor* was the least resistant to drought and *P. jeffreyi* was the most resistant with *Libocedrus decurrens* and *P. ponderosa* somewhere in between. However, without additional testing one cannot assume that the behavior of the canned seedling, grown in the greenhouse, will be duplicated in the field. Only a small difference in the relative root growth rate of these species under field conditions would be required to alter the picture. For example, if *Abies concolor* seedlings developed more extensive root systems in a particular soil than did *P. jeffreyi* seedlings, then seedlings of *Abies concolor* might never be sub-

jected to soil drought as would *P. jeffreyi* seedlings.

Nevertheless most ecologists familiar with the distribution of these four species in California would probably rate *P. jeffreyi* the most drought resistant and *Abies concolor* the least resistant. *Abies concolor* is rarely found on dry sites and is particularly favored on northern exposures while *P. jeffreyi* is often found on the driest of sites.

The relative response of these four species to spray at night was entirely unexpected. The lack of response of *P. jeffreyi* and the marked response of *Libocedrus decurrens* are not readily explained.

Summary

1. *P. ponderosa* seedlings, growing in sandy loam, reduced the moisture content of the soil to one percent below the permanent wilting point of the sunflower. When growing in clay loam this did not occur and the seedlings died when the moisture content was still one percent above the permanent wilting point.

2. Artificial dew (spray) at night prolonged the life of *P. ponderosa* seedlings by 3 months in the sandy loam and by 2 months in the clay loam after the soil moisture content had been reduced on the sandy loam to one percent below and in the clay loam to one percent above the permanent wilting point of the sunflower.

3. In both the presence and absence of artificial dew (spray) at night *P. ponderosa* seedlings grown in sandy loam reduced the soil moisture to below the ultimate wilting point of the sunflower. However, in the absence of artificial dew a lower moisture level was reached before the seedlings died.

4. *P. jeffreyi, P. ponderosa, Libocedrus decurrens,* and *Abies concolor* survived for a considerable period of time after the ultimate wilting point of the sunflower had been reached. Their survival decreased in the order named. Under the conditions of the study *P. jeffreyi* survived an average of 95 days, *P. ponderosa* an average of 64 days, *Libocedrus decurrens* an average of 44 days, and *Abies concolor* an average of 35 days.

5. Artificial dew (spray) at night increased the length of time *P. ponderosa, Libocedrus decurrens* and *Abies concolor* survived after the soil moisture had been depleted to the ultimate wilting point of the sunflower, but had no effect on the survival of *P. jeffreyi.* Dew extended the survival time 30 days for *P. ponderosa,* 20 days for *Abies concolor,* and 72 days for *Libocedrus decurrens.*

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ESTABLISHMENT OF *GRIMMIA LAEVIGATA* ON BARE GRANITE

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Introduction

The sequence of plant succession in many situations, such as bodies of water, exposed rocks, abandoned fields, burned and eroded areas, has been determined with reasonable accuracy. It is known that certain species of lichens and mosses are capable of surviving and growing directly on exposed rocks and initiating a series of plant communities that may eventually lead to communities similar to those occupying the better sites of a region. Cooper (1913), in his study of such a situation on Isle Royale, thought that the crustose and foliose lichens preceded and prepared the way for the mosses which followed. Oosting and Anderson (1937, 1939), and Keever, Oosting and Anderson (1951) found crustose and foliose lichens usually present on the exposed granite rocks studied in North Carolina, but found that they do not necessarily precede the first mosses. The pioneer mosses, usually *Grimmia laevigata* (Brid.) Brid. in the Piedmont and low mountain regions and *Rhacomitrium heterostichum*

(Hedw.) Brid. var. *ramulosum* (Lindb.) Jones and *Andreaea rothii* Web. and Mohr. in the mountains were observed and photographed growing directly on granite without being preceded by lichens (Fig. 1). In the North Carolina studies it was shown that succession on rock never proceeds without the presence of a moss and so mosses should be considered the true pioneers in this succession.

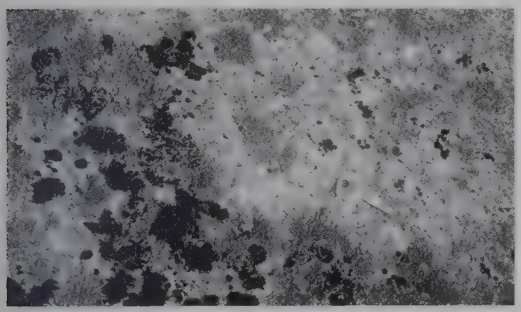

FIG. 1. *Grimmia laevigata* on granite. Black dots and patches are Grimmia; grey, smooth splotches are growths of the crustose lichen, Staurothele; patches of foliose lichens are Parmelia. Note that most of the Grimmia starts directly on bare granite and that Parmelia often grow on top of the larger Grimmia patches.

It is easy to understand why other plants will not grow on bare granite until the pioneer mosses build enough soil to hold some moisture. The hard part to understand is how these pioneer mosses live and grow in such places. Laboratory experimental methods were considered as a possible way of solving the problem of how these mosses live and reproduce.

In the fall of 1951 an attempt was made to grow the three pioneer mosses, Grimmia, Rhacomitrium, and Andreaea from vegetative shoots in the laboratory. No spores of these species were available at that time. There are large areas of *Grimmia laevigata* which have rarely been observed to produce sporophytes, and it is believed that much of the spread of this species takes place in some vegetative manner. Shoots of each of the mosses were placed in petri dishes on a nutrient solution with 2 per cent agar. Shoots of each moss were also placed on thin pieces of freshly cracked granite in petri dishes, and others on wet filter paper in such dishes. All cultures were kept under similar laboratory conditions. About three weeks later protonema, which had originated from the shoots, was observed in all of the Grimmia cultures, and numerous small branches were also growing from the original Grimmia shoots. No sign of vegetative growth was evident in the Rhacomitrium or Andreaea cultures at that time. Further experimental work was confined to Grimmia, and, since this species grows naturally on granite, that medium was used in most of the experiments. Experiments were designed to study the manner of growth of this moss and to test the effects of variations in environmental factors on its vegetative growth and reproduction.

METHODS

Manner of growth

Thin sections of freshly cracked granite were broken with a hammer into sizes that would fit into a closed petri dish. The Grimmia used in the experiments was collected from Rocky Face Mountain, Hiddenite, North Carolina (Keever, Oosting, Anderson 1950). Since much Grimmia was needed, many different clones were used. Freshly collected Grimmia was separated into single shoots, washed in distilled water, and ten strands placed on a piece of granite in each petri dish. All side branches were removed from the Grimmia shoots. The side branches are not numerous and the operation usually consisted of separating several strands that were joined near their bases. A few very small green buds too small to be removed with forceps were sometimes present just above the rhizoids on the strands placed in the culture dishes. Enough distilled water was placed in the dish to touch the bottom of the granite. The dishes were left closed except when opened from time to time to allow the addition of water as needed to keep it at the original level. Each week from February 24 to March 22, 1952, six cultures were set up in this manner.

Temperature and light

Three of the six petri dishes prepared each week were kept inside the warm laboratory and three were placed on a shady balcony outside the building. Each set of three was stacked so that some variance of light in the petri dishes was attained, with the top dish receiving the most light and the bottom one the least. No measurements were made of light intensities or temperatures because of the great daily and seasonal variations.

In a later experiment during the summer of 1952 the effect of different temperatures was again tried. Twenty-one cultures were prepared and kept for six weeks in a room where the temperature stayed constantly at 80°F. These petri dishes were not stacked so each received the same amount of light. A like number of cultures was kept in a laboratory where the temperatures were often more than 100°F.

Parts of moss plants

In the preceding experiments whole strands of moss including rhizoids, stems and leaves were used. The preliminary test had shown that most of the new shoots and protonemata originated from the stem near the bottom of the plant just above the rhizoids. Cultures were set up to see if this would hold true in separated sections of the plants. Moss plants were cut and the bottom third of the shoots placed in one culture dish and the top two-thirds in another. The tips of other plants, including mainly leaves and leaf fragments with only small amounts of the tips of stems were placed in other culture dishes. These cultures were watched for the formation of protonema and new shoots.

Substrate

All of the preceding trials were made using freshly cracked, rough granite from Rocky Face Mountain in Alexander County, North Carolina, where a study of plant succession had been made (Keever, Oosting, Anderson 1951). This granite is relatively soft and is rarely used for commercial purposes except road building. It was thought that variations in the kind of granite or other variations of the substrate might influence the growth of Grimmia. Small pieces of very hard granite quarried at Elberton, Ga. were secured from a local monument firm. Some pieces of this Elberton granite were rough and some were polished. Small pieces of granite upon which either *Staurothele diffractella* (Nyl.) Tuck. or *Parmelia compressa* (Ehrh.) Ach. was growing were collected from Rocky Face Mountain. These two lichens are the most common ones that grow directly on granite, and upon which Grimmia sometimes grows. Petri dish cultures of Grimmia were set up in triplicate and kept unstacked in the laboratory. The following variations in substrates were used: (1) rough freshly broken Rocky Face granite, (2) rough freshly broken Elberton granite, (3) polished Elberton granite, (4) Rocky Face granite covered with Staurothele, (5) Rocky Face granite covered with Parmelia, and (6) bare petri dish with no other substrate.

Culture of herbarium specimens

Dry Grimmia growing naturally on exposed granite looks grey and dead, but with the addition of water the plants quickly become turgid and green. These plants certainly remain alive for long periods of time without much water. In order to test the length of time the species remains viable without the addition of water, plants that had been in herbarium packets one year were placed in culture dishes to see if they would grow. When all of the one-year-old plants produced protonema, new shoots or both, samples were removed from herbarium specimens of all collection dates available in the Duke Herbarium and tested for viability. Nutrient agar was used as a medium for this trial because the preliminary tests had shown that Grimmia makes excellent growth on this medium and that the detection of protonema is easier on it than on granite.

Water

Experiments testing the effect of variation of temperature, light and substrate on the growth of Grimmia had all been carried out in closed petri dishes where the relative humidity was kept at or near a hundred per cent. Certainly, the available water on exposed granite where this moss grows naturally is usually very low both in the rock and the surrounding air. Before a reasonable explanation of how this moss is able to survive and spread over bare rock is gained, some understanding of the minimum amounts of water for survival and reproduction must be known. Some early experimental work had given clues that protonema and new shoots might also be very drought resistant. To determine the frequency of wetting necessary for the formation of protonema, moss cultures on rough granite were set up in open petri dishes in a laboratory, watered with distilled water so that enough water was left in the dish to come in contact with the bottom of the piece of granite. The dishes were left open and watered at varying intervals by gently sprinkling each piece of granite with enough water to restore the original level. The intervals between waterings varied from one to thirty days. It was never possible to select pieces of granite that were exactly the same shape and size, consequently the length of time a piece of granite stayed saturated after watering did not vary exactly with the watering intervals, but roughly approximated it. At the end of forty days the cultures were examined for evidences of protonemata.

To determine the effect of drought periods on the behavior of established protonema, pieces of moss were kept in closed petri dishes on granite for three weeks until fair protonemata were present on most of the pieces of moss. Then the dishes were opened and those pieces of moss on which no protonema could be seen with the binocular were removed. Two of the cultures were watered at each of the following intervals of days: three, six, nine, twelve, fifteen, eighteen, twenty-one, twenty-four, twenty-seven and thirty. At the end of forty days each culture was tested

for the presence, abundance, and condition of protonema.

Culture from spores

A continued search was made to find sporophytes of Grimmia, and many young ones were found on the west-facing slopes of Rocky Face Mountain in March, 1952. These sporophytes seemed to be mature by early May. Spores were placed on various media and examined from time to time for evidences of germination. As these early attempts to germinate spores failed, cultures were set up at intervals during the summer and following fall.

Results

Manner of growth

Five days after the first vegetative cultures were set up a few white filaments were observed on some of the moss plants in one of the petri dishes in the laboratory. These filaments had the appearance of fungal mycelium when observed without magnification, but under the microscope showed the oblique cross walls indicative of moss protenema. Within a week after the first appearance of the white protenema, it turned green. Most of the cultures in the warm laboratory showed the first protonema at between eight and twenty-one days, with the average time for the first appearance being thirteen days and the longest time being thirty-two days.

More protonema was formed near the base of moss strands when entire pieces were used and also when cut sections were cultured. The basal part of the moss was the location of most of the new shoots. The first protonema usually originated from the point of union of the new shoot and the original strand, and formed "inverted umbels" from that point to the rock below it. Protonema was occasionally observed originating from stems at locations other than the base of new shoots, but no protonema was ever observed originating from leaves. In the cut sections, the top two-thirds produced some protonema, but no shoots were observed on these sections. The tops of the plants, which were mainly leaves, produced only scattered bits of protonema and those were on pieces that evidently had more of the stem present than other pieces.

Protonema in the closed cultures continued to grow so that by the end of three or four weeks it had branched and spread over much of the plant and out over the granite for as much as an inch. Older portions of the protonema gradually turned light brown and corky-looking while the distal portions remained green and continued to spread over the granite. Three months after the cultures were set up, some of the protonema were three inches long. No buds were observed originating from the protonema, although some of the cultures were kept longer than six months. The few small shoots that had not been removed from the bases of the original plants continued to develop and others appeared until at the end of two or three weeks the young shoots were clearly visible without magnification. The distal leaves of the original strand often turned brown and seemed dead, but the young shoots grew, forming a cluster of small plants. Some plants in the closed cultures which never showed the presence of protonema produced numerous and vigorous side shoots. Ninety-four per cent of the 150 plants in the closed culture dishes kept in the laboratory from February to May produced either protonema or buds, and most of them had both. The other six per cent turned brown and died without any evidence of growth.

When the preliminary experiment showing that it was possible to grow Grimmia on granite was concluded, those pieces of granite with the moss growing on them were removed from the petri dishes and placed on a laboratory shelf, where they remained unwatered for more than a month. At the end of that time the original plants looked rolled, brown, and dead, and no young shoots or protonema were visible to the eye. In the process of housecleaning in the laboratory these pieces of granite were unintentionally placed in water with surprising results. The entire plant unrolled, the young shoots became bright green and the protonema clearly visible without magnification. The original leaves showed some evidence of being green, but much less than did the shoots. The protonema was closely appressed to the granite, quite corky looking near the original plant, but bright green near the ends. This protonema was different in several ways from the protonema on plants that had been kept continuously in closed petri dishes. That in the closed dishes had a tendency to grow upright rather than appressed to the granite, and semed to have much less of the corky protonema. Attempts were made to lift the strands of moss with the attached protonema from the granite with forceps; this was accomplished without difficulty with the specimens grown in the closed dishes, but was almost impossible to do with those specimens which had been dried. These dried specimens seemed to be glued to the granite by the corky protonema. Further attempts were made to test the adhesive force of protonema. Pieces of granite with the attached moss were submerged and agitated in water to see if the

moss would remain fastened. Strands of moss without protonema floated away from the granite and ones with protonema adhered when the rocks were merely submerged. When the rocks were agitated in water, some pieces with protonema dislodged, but the ones with the most extensive protonema remained attached. Those specimens which had been dried and possessed much corky protonema all adhered to the granite when submerged in water and when agitated, and even when held at an inclined angle under fast running water from the faucet. These pieces of once discarded granite with attached moss were kept for about six months open in the laboratory and watered and examined about every month. When finally discarded, the shoots and protonema were still living and vigorous looking after waterings.

Temperature

The weather during February and the first half of March, 1952, was excessively cold for Durham, N. C., with freezing temperatures almost every day. No protonema was observed during this cold weather in the cultures that were kept on the outside balcony, but young shoots were developing from the original moss strands in greater number and vigor than in the corresponding dishes in the warm laboratory. About the middle of March the weather turned suddenly warm with daily temperatures in the high eighties and no daily minimums as low as freezing. Within ten days after the beginning of the warm weather, protonemata were noticeable in all cultures on the balcony, with little difference in amounts in the cultures set up at different times.

In the experiment where 21 cultures (ten pieces each) were kept in a room where the temperature was constantly 80°F. and another 21 cultures in a room where the temperature was often more than 100°F., the plants in the cool room showed greater survival, more new shoots, and more protonema than those in the hot room. In the cool room 76% of the plants produced protonema, 67% produced young shoots, 27%, although producing no new shoots, were still green at the end of six weeks, and only 6% were brown and dead looking. In the hot room only 47% produced protonema, 51% showed new shoots, 22%, although producing no new shoots, were still green at the end of six weeks, and 27% were brown and dead looking.

Light

In the three-tiered stacks of petri dishes, both in the warm laboratory and on the cool balcony, protonema began to develop in the dish on the bottom of a stack several days before it did in the top dish. Protonema in the top dish, however, turned green sooner after its development than that in the bottom dish, and continued to develop and spread over the granite more vigorously than those in the bottom dish.

Substrates

There was little difference in the number of pieces of moss producing protonema and new shoots on the several substrates, but slight differences in the behavior of the moss plants and protonema were noticed. The protonema seemed to spread more quickly and further over the polished granite and glass than over the rough granite, but did not hold the plants to the substrate as securely. On the polished granite about half the pieces of moss with evident protonema floated when the rocks were submerged in water, and none adhered when the rocks were agitated in water. Protonema was formed on about half of the pieces of moss on the bare glass, although some difficulty was experienced in keeping the glass surface damp; several of the plants without protonema as well as most of the ones with protonema stuck to the glass when the dishes were submerged in waer, but all failed to adhere when the dishes were agitated in water. Protonema was slower in spreading over both kinds of rough granite, but the adhesion to the rough rock when submerged in water seemed to be proportional to the amount of protonema present, and those plants with much protonema adhered to the rough granite even when agitated vigorously in water. The pieces of moss growing on the two kinds of lichens showed initial production of protonema and young shoots comparable to those produced on the clean granites. However, after four weeks most of the original moss plants and young shoots on the lichens looked brown and partially decayed, and protonema was more abundant and vigorous on the sections of the rocks which had less of the lichens present. There were no differences in the behavior of the moss plants on the soft Rocky Face granite and on the harder Elberton Granite.

Age of specimens

Table I shows the percentages of moss plants of the various ages that produced either buds or protonema, thus showing evidences of life and ability to reproduce. Fifteen plants were used for each age class.

Water

Protonemal formation was never as abundant or noticeable in the open dishes as in the closed ones. Even with as gentle sprinkling as possible, some pieces of moss were washed off the rocks,

TABLE I. Viability of Grimmia specimens taken from herbarium packets. Fifteen moss strands from each collection were cultured on nutrient agar in closed petri dishes from May to August. One collection for each age except 10 years

Age of Herbarium Specimens in Years	Percentage of Plants Growing
1	100
2	100
3	93
5	..
7	7
10 (a)	20
10 (b)	..
14, 15, 16, 17, 21, 30, 55	..

or blown off with the breezes that came in the laboratory window. The displaced pieces were picked up and replaced on the granite. Small amounts of protonema are sometimes difficult to see even with magnification. The pieces of granite were agitated in water at the end of the experiment and if a piece of moss adhered to the rock, this was taken as partial evidence that protonema was present.

Table II shows evidences for protonemal formation at the end of forty days in the dishes watered at different intervals. Protonema was definitely seen on some of the pieces of moss in the cultures marked "+." No protonema was actually seen at the end of forty days in the cultures marked "?," but some of the pieces of moss adhered to the granite when agitated in water. No protonema was seen, and no pieces of moss adhered to the granite when agitated in water, in the cultures marked "—."

Table III gives the results of the experiment testing the effect of different watering intervals on the behavior of established protonema. Many of the protonemata on the strands of moss which were watered frequently either did not survive or did not become attached to the granite. The longer a moss plant with established protonema stayed dry, the more firmly it was fastened to the granite.

Germination of spores

Attempts to germinate Grimmia spores from capsules matured in May 1952 were continued at intervals through the summer with no results. In October, spores germinated on all media, including granite, and formed protonema similar to that produced from gametophyte parts. No buds were ever seen on this protonema although the cultures were kept more than six months.

TABLE II. Evidence of protonema formed from Grimmia shoots on granite in open petri dishes watered at indicated intervals. Cultures started April 8, ended May 16. +, definite; —, none; ?, questionable

Days Between Waterings	Presence of Protonema
1	+
2	+
3	+
4	+
5	?
6	+
7	?
8	+
9	—
10	?
11	—
12	?
13	+
14	—
15	?
16	?
17	?
18	—
19	?
20	?
21	+
22 to 30	—

TABLE III. The effect of drought periods on the behavior of established protonema. Twenty-two petri dishes cultures with ten pieces of moss each were set up March 16, and kept closed until April 9. Plants showing no protonema were removed. Two of the opened cultures were watered at each of the indicated intervals. May 16, the cultures were tested for adhesion of moss to the granite

Days Between Waterings	No. of Plants With Protonema at Beginning of Watering Intervals	Plants Adhering When Submerged in Water		Plants Adhering When Agitated in Water	
		No.	%	No.	%
1	18	7	37	6	33
3	17	4	24	4	24
6	16	6	37	6	37
9	17	6	40	5	36
12	15	12	80	7	47
15	18	10	55	8	44
18	15	11	73	10	66
21	17	13	76	8	41
24	15	12	80	8	53
27	15	13	87	11	73
30	14	14	100	14	100

CORRELATIONS

Observations had previously indicated that *Grimmia laevigata* is capable of growing directly on exposed granite. Since there are large expanses of Grimmia that seem rarely to produce sporophytes, it is suspected that some vegetative means of reproduction is largely responsible for the propagation of the species. These laboratory experiments have shown that the moss can be grown vegetatively on freshly broken granite. Under favorable laboratory conditions abundant protonema is formed from the stem of the gametophyte, spreads over the granite and acts as an

adhesive force holding the moss to the rock. No buds were observed arising from this protonema in these experiments but numerous new shoots grew from the original moss strand, forming small colonies of the plants. The formation of protonema and new shoots was much more abundant from the basal part of the moss strands than from the upper parts of the stem, even when the strands were cut into separate sections before culturing. The moss grew equally well on both hard granite and soft granite. Protonema was produced in about equal amounts on rough and on smooth granite, but had a greater tendency to stick to the rough granite. Grimmia also grew on top of the two most common lichens on exposed granite, but with noticeably less vigor than on clean granite.

No protonema was formed when the temperatures were frequently below freezing, but such cold weather did not inhibit the growth of new shoots. Protonema was formed more quickly in reduced light than in stronger light, but did not turn green as quickly or grow as well in reduced light.

Protonema was very abundant and vigorous on plants that were kept where the relative humidity was continuously high, but continuous high relative humidity is not necessary for the formation of protonema. Both protonema and new shoots were usually formed on plants that were wet only every four or five days, and sometimes on plants that were watered as infrequently as fifteen or twenty days. Established protonema is very drought resistant and lives at least a month without the addition of water. These periods of prolonged drought increased the adhesive power of the protonema in proportion to the length of the period without water. Mature gametophytes can live long periods of time without water. Herbarium specimens two or more years old grew as well or better than freshly collected materials, and some pieces of moss were viable after as long as ten years in a herbarium.

It would be difficult to observe and record the behavior of a given piece of moss on a granite outcrop, but these laboratory experiments present a key to what might and probably does happen there. A piece of Grimmia, even a small basal piece of the plant that has been moved to a new location on granite by wind, water, or some other force, could produce new shoots and form a new colony of the moss held in place by protoema, if the right combinations of environmental conditions existed. These favorable conditions seem to be: (1) wetting of the piece of moss by rain or heavy dew at least every four or five days during a period of two or three weeks without currents of water or wind strong enough to move the strand, (2) cool, cloudy, but not freezing weather for the two or three weeks indicated in condition 1, and (3) a subsequent period of dry sunny weather.

Such a set of conditions may occasionally happen, probably in the spring or fall of the year. The one specification most often violated, especially when the others are present, would be the absence of moving wind or water that would shift a loose piece of moss from place to place. The minute rough places on the granite might provide enough friction to stop the moving pieces if the force of the water or wind were small. Even though it might be years before the exact set of conditions are met, the fragments of moss could remain alive and capable of growing. It seems reasonable to assume that this happens often enough to be partially responsible for the establishment of new colonies of Grimmia. It cannot be claimed that this vegetative propagation is the only means of spreading the species because sporophytes are produced in some places and protonema from the spores will germinate and grow directly on granite. Because gametophytes were not observed originating from such protonema under laboratory conditions does not prove that they are not produced from it at some times under natural conditions. Whether produced from gametophyte fragments or from spores, new colonies of Grimmia do start directly on granite, and once a colony is anchored to the rock it enlarges and spreads over the granite forming large mats which coalesce with other mats to form the extensive Grimmia covers upon which further succession of plants proceeds.

Summary

Grimmia laevigata (Brid.) Brid., one of the pioneer mosses in xerarch succession of plants on granite in North Carolina, was grown from gametophyte shoots on pieces of freshly cracked granite in petri dishes. Protonema arises from the stem, spreads over the rock and causes the plant to adhere firmly to the substrate. No new plants were observed arising from such protonema, but many new shoots originate from the stem of the gametophyte and form a colony that is held on the granite by the protonema. Experiments were performed to test the effects of variations of environmental factors on the growth of protonema and new shoots with the following conclusions:

1. Protonema is formed abundantly in cool, but not in freezing temperatures.

2. New shoots grow vigorously in low temperatures, this growth not being permanently halted

by temperatures dropping frequently below freezing.

3. Protonema forms faster in reduced light than in bright light, but develops chlorophyl faster and continues to grow more in strong light.

4. Grimmia grows better on granite without lichens than it does on granite with lichens.

5. Protonema adheres more firmly to rough granite than to smooth granite.

6. Protonema is usually formed if a piece of moss on granite is wetted every four or five days for a period of two or three weeks.

7. Long periods of drought do not kill protonema and the longer that established protonema remains dry, the more firmly it sticks to the granite.

8. Most herbarium specimens of Grimmia are viable for as long as three years and some ten-year-old specimens will grow.

With this evidence there should be no reason to doubt that this moss can become established on bare granite if the right combination of environmental factors is present.

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THE VEGETATION OF NORTHERN MANITOBA
II. A PRISERE ON THE HUDSON BAY LOWLANDS

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Introduction

There have been very few studies of the vegetation of subarctic Canada. Accordingly, the immediate objectives tend to be rather in the field of plant geography than plant ecology; that is, the first steps are to provide descriptions of the communities which comprise the major vegetation zones of the area, to determine the limits of these zones, and to reveal the directions which further, strictly ecological work should follow. These are the primary aims of the present series of investigations, which is confined at present to the vegetation of northern Manitoba. This paper purports merely to present certain geographical facts concerning part of the vegetation of this area, and to suggest a working hypothesis by which these facts might be interpreted and from which further, more critical studies will ensue.

In certain regions of the Hudson Bay Lowlands there are considerable deposits of granular, calcareous glacio-fluvial material. These are common in the estuary of the Churchill River (58° 47'N., 94°11'W.) where the greater part of the observations which are reported here have been made. Along the east shore of the estuary there are extensive river flats where young granular deposits are being exposed and subsequently colonized by vegetation. This process is regulated by the deposition of alluvium and, less rapidly, by the recession of the level of Hudson Bay. At this site there is a distinct zonation of vegetation which forms bands which run parallel to the river shoreline (Fig. 1). It is suggested here that these zones represent the sequence of vegetation change which takes place, and which has taken place in the past, on many of the lowland sites of this region.

The terrain of the Hudson Bay Lowlands consists of uplands, represented in this area by outcrop ridges (rare), gravel ridges and hills, and raised beaches; as well as lowlands which consist of extensive glacio-fluvial deposits (cf. Cheney and Beckel 1955 and Coombs 1954). The latter, under the influence of both the sedimentary Palaeozoic limestone and the conspicuous marine component which has resulted from a period of submergence, are highly calcareous. At Churchill there is evidence of the continuous encroachment of vegetation on to the contemporary river flats; it is this sequence of communities which will be described here. No attempt will be made to described the divers communities which occur on upland and certain other lowland sites, nor is it appropriate here to present a detailed, analytical account of the communities which form the prisere which is being outlined. The primary objective of this preliminary account is to point out the major features of this prisere, to indicate the pos-

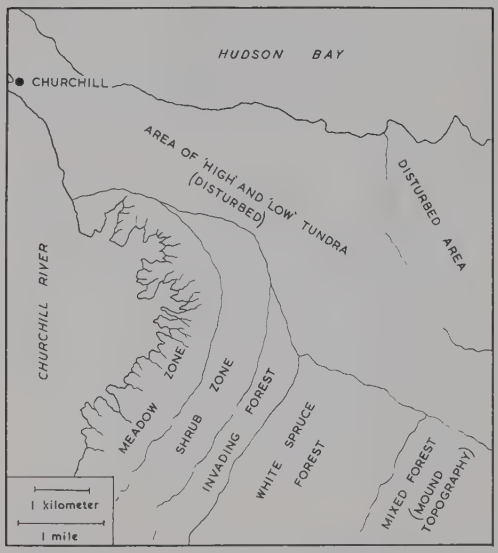


FIG. 1. An outline map of the immediate precincts of the East side of the estuary of Churchill River, showing the approximate boundaries of the zones of vegetation which are described in the text. These boundaries have been determined by reference to certain vertical aerial photographs which are available for this area.

sible significance of these findings in the interpretation of the ecological relationships of the tree-line dominants of the area—*Picea glauca* and *P. mariana*—and to align this work with recent reports from other parts of North America.

These investigations are being supported by generous grants from the National Research Council of Canada. I wish to record my thanks to the Defence Research Board of Canada for permission to use the excellent facilities of their Northern Laboratory at Fort Churchill.

THE EVIDENCE OF SERAL CHANGE

The first closed community on the most recent flats is a meadow which covers considerable areas and is interspersed with small pools and streams. It occupies the zone immediately above the high-tide level, and extends inland for ½–1 km. The chief grasses of this community are *Festuca rubra,* Hierochloe odorata* and *Puccinellia paupercula;* these are associated with *Aster puniceus* var. *firmus, Cardamine pratensis, Carex limosa, C. rariflora, C. vaginata, Juncus arcticus, J. balticus, Parnassia multiseta, Lomatogonium rotatum, Argentina pacifica, Plantago maritima, Senecio pauperculus, Triglochin maritima* and *T. palustris.* In small shallow pools, the more common colonizers are *Triglochin maritima,* which forms compact tussocks, and the aquatic plants *Hippuris tetraphylla* and *Ranunculus purshii.*

Adjacent to this meadow community is a broad shrub zone (Fig. 1). At the lower limit of this zone young plants of *Salix brachycarpa* var. *antimima* are actively invading the meadow. Further inland, *S. alaxensis* and *Betula glandulosa* appear, and these three shrubs form a dense community, associated with the greater number of the meadow species. Throughout the shrub zone are numerous small pools and wet depressions.

In the older regions of this shrub zone are many seedlings and young trees of both *Picea glauca* and *Larix laricina.* The seedlings of the former are rooted in the mossy humus which accumulates at the bases of moribund dwarf birch and willow shrubs. With increasing distance from the river, the stature and density of the spruces and larches increase, and ultimately a closed coniferous forest stage is reached. In this forest, and in the invading front, the ratio of spruce individuals to larch varies from approximately four to one to eight to one. Some indication of the spatial arrangement of the invading, peripheral zone of the forest can be gained from an examination of Figures 2 and 3. The heights, diameters (at breast height) and ages of the trees plotted in Figure 3 have been tabulated in Table I. The ages were determined from the microscopical examination of two cores taken from the south-facing side of each tree, using a Swedish increment borer. It is clear that *Picea glauca,* and to a lesser extent *Larix laricina,* are actively invading the shrub zone of the river flats. Behind this invading front there is a white spruce forest which occupies a zone of 3-4 km. in breadth (Fig. 1).

This coniferous forest consists of an upper stratum dominated by well-grown trees of *Picea glauca,* with which are associated scattered indi-

FIG. 2. A view of the uneven aged community of the invading front of the forest, here made up largely of *Picea glauca.* The shrub layer is composed of *Salix brachycarpa* var. *antimima, S. alaxensis* and *Betula glandulosa.*

* Nomenclature as in Ritchie (1956).

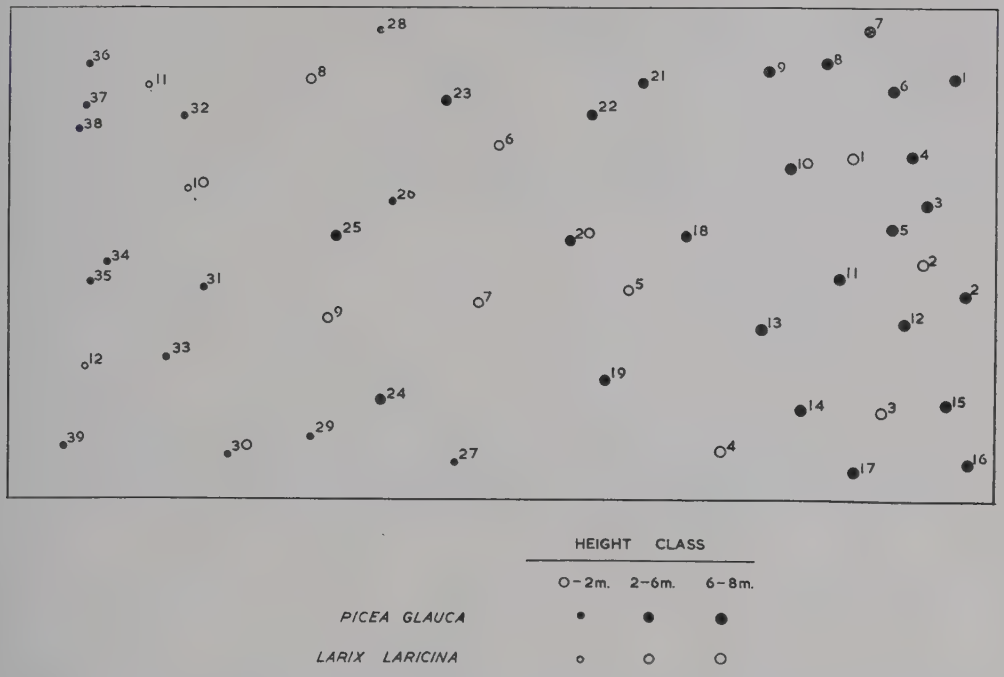


FIG. 3. A quadrat chart (50 m. x 25 m.) across the invading front of the forest, showing the spatial arrangement of the trees. The numbers correspond with those of Table I in which data of age and stature are found.

viduals of *Larix laricina*. Locally a discontinuous shrub stratum of *Betula glandulosa* and *Salix brachycarpa* var. *antimina* is present. The ground vegetation of wetter sites consists of a carpet of mosses, of which *Tomenthypnum nitens, Hylocomium alaskanum, Pleurozium schreberi, Dicranum groenlandicum, D. elongatum* and *Aulacomnium turgidum* are conspicuous. On drier sites the ground vegetation is dominated by a lichen carpet, composed of *Cladonia alpestris* and *C. rangiferina*, associated with *Stereocaulon paschale*. Common in the more shaded parts of the forest and listed in approximate order of abundance are *Vaccinium uliginosum, Carex leptalea, Salix reticulata, Ledum groenlandicum, Vaccinium vitis-idaea* ssp. *minor, Empetrum hermaphroditum, Pedicularis labradorica, Tofieldia pusilla, Moneses uniflora, Orchis rotundifolia, Bistorta vivipara, Carex concinna, C. gynocrates* and *Petasites sagittatus*.

Throughout this community are small peaty depressions, associated with peat hummocks or small mounds. The surfaces of the latter, characteristically, bear a lichen carpet, and locally these mounds with lichen cover are extensive; associated with these areas the spruce stratum is more open, forming small patches of "lichen woodland" or taiga. In the depressions are various aquatic and semi-aquatic plants, of which *Carex stans, Ranunculus purshii, Senecio pauperculus* and *Myriophyllum exalbescens* are typical. The substratum under this white spruce community consists of an upper layer, 50-100 cm. in depth, of spongy black peat, overlying the calcareous material of the old river flats and beaches.

At this tree-line locality, the performance of *Picea glauca* seems to depend closely on the local topography and the substratum. For example, on the sheltered flanks of a large gravel ridge, a tree of 180 years measured 16 m. in height and 30 cm. in diameter at breast height; on the sheltered, south-facing sides of the outcrop ridges an average tree of 157 years is 10 m. tall and 22 cm. in diameter at breast height. However, on the seaward, exposed outcrop ridge slopes, where there is a thin soil, reduced snow cover in winter, and considerable exposure to the prevalent northerly winds, small trees predominate with multiple, trimmed trunks and extensive *krummholtz*. By contrast, the site of the present study is of one of both relatively good soil conditions and considerable shelter. The trees of this lowland forest are symmetrical, in contrast with the severely

TABLE I. The dimensions and ages of the individuals of *Picea glauca* and *Larix laricina* which have been plotted in Figure 2, from the sample area studied in the invading front of the coniferous forest zone

	PICEA GLAUCA			PICEA GLAUCA			
No.	Height (m.)	d. b. h. (cm.)	Age	No.	Height (m.)	d. b. h. (cm.)	Age
1	8	15	97	28	1.5	5	15
2	9	20	125	29	1.5	4	13
3	7	13	75	30	2	5	17
4	7.5	14	98	31	2	5	25
5	8	15	106	32	1.5	4	16
6	9	21	126	33	1.5	4	18
7	8	16	105	34	1	4	14
8	7.5	12	99	35	1	4	15
9	10	16	134	36	1.5	5	17
10	6.5	12	99	37	1	3	13
11	7.5	19	109	38	2	5	19
12	7	14	88	39	1	4	16
13	8	14	116				
14	7	12	96	LARIX LARICINA			
15	6	12	89				
16	7	13	96	1	8	13	85
17	6	14	80	2	7.5	11	76
18	6	15	51	3	8.5	14	98
19	4	12	40	4	8	12	58
20	3	9	37	5	7	10	41
21	5	11	44	6	5	8	34
22	5.5	10	43	7	6	7	26
23	6	9	59	8	4	7	29
24	3	9	34	9	3	6	18
25	4	10	38	10	2	5	15
26	2	7	25	11	2	5	15
27	2	6	18	12	4	4	14

trimmed trees on the outcrop ridge a few kilometers distant.

With increasing distance from the river flats, certain notable changes in vegetation and topography are perceptible. The hummock-hollow pattern which is present in varying degrees throughout the meadow, shrub and white spruce forest zones is replaced by large mounds of peat with intervening depressions which often contain standing water. These mounds, depicted in the lower part of Figure 4, are 2-4 m. in height (above the level of the surrounding low areas) and 12-25 m. in diameter. It is in this region of topographic change that *Picea mariana* is found—it is completely absent from the younger communities on shallow organic material. A consistent observation was that the smaller mounds bear an open mixed stand of *P. glauca* and *P. mariana*, of which the former tends to occupy peripheral positions. In late summer, it was possible to detect permafrost at a depth of 1 m. in the centre of the mounds. Concomitant with the black spruce are certain characteristic species which also are completely absent from the earlier stages of the sequence; of these *Sphagnum fuscum, S. warnstorfianum, Carex canescens, Rubus chamaemorus, Myrica gale* and *Andromeda polifolia* are the most common.

At a greater distance from the river these mounds are of greater size, and *Picea mariana* becomes more abundant, dominating the central regions while *P. glauca* is confined to the periphery. In these situations, many of the individuals of white spruce are conspicuously tilted away from the centres of the mounds, indicating that the growth of the mound and encroachment of the surrounding lake-bog have caused displacement from a vertical position. Age determinations of trees of the two spruce species showed that the white spruces, often moribund, are older, reaching 250 years, while the black spruces form stands of uneven age including relatively young trees. On the oldest completely forested mounds, the central areas are occupied by black spruce trees of the "candelabrum" habit which is depicted in Figure 4. At this stage the lower limit of the active layer of permafrost was located at 60 cm. in mid-August.

The vegetation of the upper parts of the mounds, under the discontinuous black spruce canopy, consists of a dense lichen carpet in drier places, dominated by *Cetraria nivalis, Cladonia alpestris* and *C. rangiferina*, of which *C. alpestris* often forms lichen polygons, and of moss carpets and hummocks in damper situations, largely made up of *Sphagnum fuscum, S. warnstorfianum, Pleurozium schreberi, Dicranum elongatum*, and *D. bergeri*. Associated with the cryptogamic facies are *Ledum groenlandicum, Vaccinium vitis-idaea* ssp. *minor, Rubus chamaemorus, Oxycoccus microcarpus, Kalmia polifolia* and *Carex canescens*.

The tree cover of the large mounds at still greater distances from the river is represented solely by *Picea mariana*. These mounds are found in the regions beyond the southeast corner of the area shown in Figure 1—for example, they are common along the East side of Farnworth Lake.

The major aspects of the vegetation and topography which are described above are summarized in the diagram shown in Figure 4. It is suggested here that the different zones of vegetation which can be recognized in this area at Churchill, represent the different stages in the sequence of vegetation which develops in certain parts of the Hudson Bay Lowlands. There is clear evidence that the white spruce forest is invading the younger, shrub-dominated flats, and that it is ultimately replaced by a black spruce community on large peat mounds.

DISCUSSION

The following is suggested as a working hypothesis by which the observed zonation of vegetation and the evidence of invasion and replace-

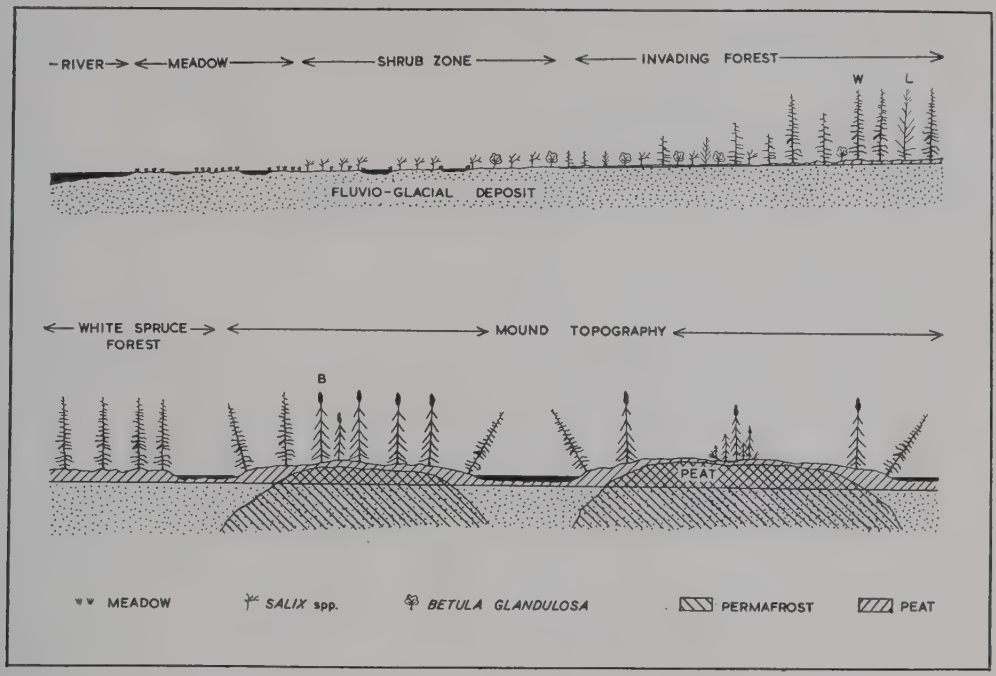


FIG. 4. A profile diagram summarizing the zonation of vegetation types which is found in the area. W, L, and B refer to trees of white spruce, larch and black spruce respectively. This diagram is a reconstruction and does not attempt to indicate either the scale of the plants depicted or the relative proportions of the vegetation zones. Continuous shading indicates areas of open water.

ment might be interpreted. After the open calcareous mineral soil of the deposits has been colonized successively by meadow and shrub phases of vegetation, a pronounced layer of peat develops; the wet conditions of the soil and the subarctic climate of this latitude favour the accumulation of organic matter as peat. These conditions are suitable for the entry of seedlings of white spruce and larch. The continued deposition of organic matter and formation of a peat layer in the substratum has a two fold influence; firstly, it insulates the ground to the extent that the level of the perennially frozen layer is raised, thereby impeding drainage and providing suitable conditions for the entry of rapid peat forming species, notably species of *Sphagnum*. Secondly, the upper layers of the peat tend to become acid, being effectively isolated from the underlying calcareous material, and further facilitating the entry of species with acid preferences. Under these conditions, *Picea mariana* colonizes the central, highest areas of the peat mounds. The poor drainage of the area results in a hummock-hollow topography. White spruce is absent from the mounds, which, by their active increase in size, displace the white spruce of the periphery; this process is accelerated by the erosion of the mound margin by the bog. The ultimate stage of this forest sequence is of black spruce dominated mounds surrounded by shallow ponds and peat bogs.

From the results of pollen analysis of certain peat samples from a deposit about 40 km. South of Churchill, Johnson (1949) suggests that the sequence of post-glacial vegetation which colonized the mineral soils of this area was from sedge-meadow, through heath and birch scrub zones, to spruce forest. The broad outlines of this sequence are similar to the prisere which is outlined here, and it would seem probable that the sequence of communities which is described might well have been common on the extensive areas of calcareous mineral soil which were exposed after the post-glacial marine inundation.

In the area of the Hudson Bay Lowlands, considering lowland sites, *Picea glauca* is entirely absent from the extensive peat-covered areas of the interior, being confined to relatively young alluvial soils along streams and rivers, and at river estuaries. Excellent stands of white spruce have been observed by the writer at Warkworth Creek, 10 km. South of Churchill, and at the estuary of the North and South Knife rivers,

40 km. northwest of Churchill, the latter site situated a considerable distance beyond the limit of continuous forest. White spruce occurs on the following upland sites in the region of the Hudson Bay Lowlands—on the well drained mineral soil abutting on the outcrop ridges, on the flanks and summits of raised beaches, and on certain large fluvio-glacial gravel deposits.

Among the scant references in literature to the vegetation of this part of the Hudson Bay Lowlands, that of Tyrrell (1898) is still the most pertinent. He describes the primary fact of the present account in the following words (p. 163): "At Fort Churchill, near the shore of Hudson Bay, small white spruce were found to have entirely replaced black spruce in the swamps. A few miles further inland, black spruce again takes its normal place in similar swamps, and white spruce almost disappears." And the same author indicates (p. 99) that the coastal plain between Churchill and Nelson River is characterized by "wide grassy plains," "low scrub of dwarf birch and willow," and sparse woodlands of white spruce and larch with larger stands of white spruce further from the coast. In a personal communication, Dr. Ilmari Hustich informs me that he has observed the replacement of white spruce communities by black spruce in areas of the Hudson Bay Lowlands in northwest Ontario.

The immediate impression gained at Churchill is that *Picea glauca* is more common at the northern limit of trees than is *P. mariana*, but when one examines areas 10-20 km. southeast of Churchill, where estuary, gravel ridge and outcrop ridge sites are absent, black spruce is the dominant tree (cf. Ritchie, 1956, p. 285). For certain areas in southeast Hudson Bay, Hustich (1950) refers to white spruce as the dominant of "the maritime tree line" and he suggests that the preponderance of "glacial till of sedimentary bedrock origin" and marine deposits account for the greater proportion of white spruce than black spruce. In those parts of the transition zone between tundra and forest which the present author has examined in northern Manitoba, *P. mariana* is confined to peat deposits and mineral soils derived from acidic, pre-Cambrian rocks, while *P. glauca* extends into the forest-tundra on certain alluvial soils—particularly those within the limestone area—and on eskers. And in these extreme situations in the forest-tundra, white spruce shows consistently better vegetative performance than black spruce. This has been attributed (Hustich 1954, Rowe 1956) to some hardier race of white spruce which reverses the relationship of southern regions where black spruce is regarded as more resistant to local climatic extremes. Instead, it may be that the soils to which white spruce is confined (alluvium, gravel deposits, eskers) are influenced to a lesser extent by the extremes of climate than are black spruce substrata which either show very poor soil development, as on the coarse rocky drift of upland sites, or are influenced by permafrost as on peat deposits.

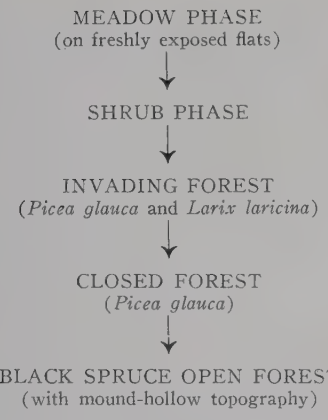
It is suggested that *P. glauca* is replaced in the prisere on the Churchill flats because it is intolerant of the acid, peat conditions. Throughout boreal and subarctic regions in this part of Canada, it has been noted (Hustich 1954, 1955, Rowe 1956, Ritchie 1956a) that white spruce is completely absent from peat substrata.

Drury (1956) has described a similar sequence of forest change from Alaska, a sequence which differs considerably from the present one in both floristic and ecological details, but which indicates the same replacement of white spruce forest on alluvial soils by black spruce muskeg. He ascribes this replacement to an increase of soil moisture conditions on older floodplain sites. However, it would appear that the operative complex of factors responsible for the changes on the Hudson Bay Lowlands is concerned with the inability of *P. glauca* to occupy the acid peat with high permafrost level on the developing mounds, which situations are favourable to the lime-intolerant *P. mariana*. The elucidation of the precise factors which control these changes, and which in fact are responsible for the apparent differences in ecological amplitude between *P. glauca* and *P. mariana*, must await more detailed studies, and ultimately, the results of experimental work.

It should be added that the ultimate cyclical sequence of black spruce muskeg and *strangmoor* which Drury (1956) describes from Alaska is present in the interior regions of the Hudson Bay Lowlands in Manitoba. Extensive lowland sites southwest of Churchill have been observed which are covered by large areas of *strangmoor*, associated with "islands" of peat (= mounds) which are covered, completely or merely at the periphery, by an open black spruce forest. These phenomena are the object of current investigations and they will be described in subsequent reports.

Summary

On certain glacio-fluvial substrata of the Hudson Bay Lowlands in northern Manitoba there is evidence of a distinct sequence of vegetation. This sequence, not universal in this geographical region, might be summarized as follows:



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THE SAVANNAH CONCEPT AND ITS USE

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Introduction

The most common image produced by the word "savannah," among students of vegetation, probably is the one given by Schimper (1903): xerophilous grassland containing isolated trees. This is the sense in which the word is used here. Schimper also described "savannah forest (tropical)," but it is not considered here. Some encyclopedias and many laymen restrict use of the word savannah to discussions of tropical vegetation. However, two recent textbooks on ecology (Odum 1953, Oosting 1956) recognize savannah in temperate climate.

A reluctance to use the term "savannah" is evident in much North American scientific literature. The 1952 index to Ecology, covering the first 30 years of publication, lists but one reference under savannah. The 1956 index to *Ecological Monographs,* covering the first 20 years of publication, has two. The *Journal of Forestry* with three cumulative indexes, covering 48 years of publication, has none. Yet, circumlocutions such as "scattered tree grassland," "pigmy woodland," "woodland range," "open forest grazing land," "forest-grassland transition," "forest range," and others, are common. Such terms may indicate that savannah types of cover are being recognized, but also that in inventories of resources they may be included under either forest or grassland with uncertain goals and standards for their management.

The known usefulness of distinguishing savannah (from forest or grassland) in everyday problems of adjustments in land-use and management suggested the need for this investigation. Problems and uses of savannah vegetation have been studied intermittently for about 20 years; first as a forester in Arizona and New Mexico and later as a range conservationist with opportunities to become familiar with all the types of savannah that border or occur in the midcontinental grasslands, from Canada to Mexico and the Gulf.

Recognition of Savannah

Places that are named Savannah, Savanna, or Sava, are of special interest. They indicate recognition of this type of vegetation by laymen at the time the places were named. Since settlements usually are named prior to great disturbance of natural vegetation, they may be indicative of origi-

nal vegetation. No state, of course, now has more than one mail or freight address by such a name. Also, since settlement was from east to west, out from forested lands toward the prairies, places named Savannah are more likely to occur at the eastern edge of the savannah than the western.

It was found that the locations of places named after savannah are most common near an area often referred to as a border between the midcontinental grasslands and the eastern forests.

If a line is drawn from north to south through the westernmost places named after this type of cover, the result provides a rough approximation of the location of savannah between grassland and forest. The places are:

Savannah, Itasca County, North Central Minnesota
Savanna, Carroll County, Northwest Illinois
Savannah, Davis County, Southeast Iowa
Savannah, Andrew County, Northwest Missouri
Savanna, Pittsburg Country, Southeast Oklahoma
Sava, Van Zandt County, Northeast Texas

There is also Savannah, Ashland County, North Central Ohio, and Savannah, Hardin County, Southwest Tennessee to indicate greater width of a belt, or outliers, through the central portion of this savannah of the Temperate Zone.

Savannahs far to the east have been described by Oosting (1956) as follows: "From the pitch pine barrens of New Jersey through loblolly pine and longleaf and slash pine in the more southern states, fire maintains pine dominance, usually in open stands, called savannahs, with the highly combustible wire grass (*Aristida stricta*), for ground cover. These stands owe their origin and maintenance to their resistance to fire. If protected from fire, they would unquestionably be replaced by oak-hickory dominated forest."

These savannahs, deep in a forest climate, need not be considered further here except to note that among place names, including Savannah, Georgia, the spelling with a final "h" is plainly the most common. It is apparent that our forebears recognized savannah in many places where it is still to be recognized today.

Curtis (1955) reported savannah characteristic at all boundaries between prairie and deciduous forest in Wisconsin. Bruner (1931) reported oak-hickory savannah extending from deciduous forests of mountainous eastern Oklahoma as far west as central Oklahoma on sandy and rocky soils. Osborn (1942) described shinnery (oak scrub) savannah at the western edge of Oklahoma where, as his illustrations show, the oak is but little taller than tall grass.

Clements (1928) recognized and named numerous types of tree savannah in the Blackhills, the Rockies, and westward into California. He also described scrub savannahs largely confined to the Southwest and Mexico. Parks were described as differing from savannahs in that communities mix by alternating areas or groups rather than by scattered individuals. Concerning fire and grazing in savannahs he wrote: "Since grasses and herbs are usually eaten to a much larger degree, intensive grazing, and especially overgrazing, will reduce their hold upon the soil and correspondingly improve conditions for the spread of shrubs. . . . while savannah is primarily an indicator of climate, its secondary indication is one of grazing and absence of fires upon which its practical utilization must be based." Under savannah, Clements included grassland with isolated shrubs as well as trees, but restriction of the concept to population assemblages of primarily grass and tree, rather than shrub, species is far more widely accepted and, I believe, much to be preferred.

Marbut (1911), eminent soil scientist, wrote concerning the Ozark Mountains: "The greater part of the Ozark Dome was up to the middle of the nineteenth century, a region of open woods, large areas being almost treeless. Except on the roughest land, the thoroughly dissected portions of the Clarkville soils, the rough stony land, the Decatur soils, and the more hilly portions of the Boston Mountain Plateau, the timber growth was not dense enough to hinder in any way the growth of the grass. The whole region in its vegetation was more closely allied to the western prairies than to the timber-covered Appalachians. . . . Live-stock farming was capable of adjustment to all the conditions without exception. . . . The growth of brush spread with great rapidity, every locality being supplied with seed-producing trees of mature age. Within a few years the greater part of the region was entirely covered with a vigorous growth of young trees, mainly oaks. The change began to take place on an important scale immediately after the Civil War. . . . At the present time great areas of woodland support an extremely small number of cattle or sheep."

Thirty years later the author (Dyksterhuis 1941) prepared a report and generalized map of the main area of savannah sites, bald knobs, and glades of the Ozark Dome. In reviewing past and then current conditions he reported, (1) fire alone and no grazing (to reduce fuel) would probably

have extended the area of grassland, (2) no fire and light grazing would probably have maintained the *status quo,* (3) no fire and heavy grazing will result in dominance of the woody species, (4) fire and heavy grazing together have hastened the dominance of the woody species." Dyksterhuis (1948), in the Cross Timbers region of Texas, described changes in relative coverage by species that accompanied deterioration of natural savannah under close grazing. Five points in the process from original open savannah to thickets were illustrated by photos in Figures 15, 20, 21, 22, and 23.

Walter (1954) recently has discussed the dangers and causes of savannahs becoming thickets in southwest Africa. Grazing is recognized as a primary factor. He clearly distinguishes between natural savannah of savannah climate, edaphic savannahs, and savannahs caused by man.

Problems and Uses of the Concept

Decisions for long-term use of land must usually be made between (1) cultivated crops, including tame pasture or tame hay in crop rotations, (2) permanent tame pasture, (3) natural pasture or range, (4) natural forest, or (5) forest plantation. It is in this connection that the savannah concept is exceedingly useful.

Lands unsuitable for cultivation because of erosion hazard or for other reasons usually will be devoted primarily either to grazing or forestry. The proper major use, and the one to govern in management decisions, ordinarily will be determined by potentialities of the soil and climate. These are best indicated by the original or climax cover. On a nonarable site where the climax cover is savannah, the proper use is most likely to be natural pasture. Nonarable forest sites are just as likely to be best suited for use as natural forest.[1]

It is generally understood that a site on which forest is climax tends always through plant succession, to return to forest cover. It it not so widely recognized that grazing, as ordinarily practiced, hastens a return to a woody overstory on forest sites; while on grassland and savannah sites a woody overstory is possible only through destruction of a natural community and an increase or invasion of woody plants through more grazing and less fire than characterized the presettlement era.

There may be some grazing on forest sites following opening of the stand but its management should be a subject for study by silviculturists. Income from grazing will ordinarily be incidental and irregular. Native pasture on nonarable forest land cannot be regarded as a permanent grazing resource as can natural grassland or natural savannah.

Foresters commonly express the combined effect of different environmental factors on tree growth as site index. The most widely used site index classifications for forest areas bordering natural grasslands of the United States are those of Schnur (1937) for upland oaks of the East, and of Meyer (1934) for ponderosa pine of the West. It is significant that the poorest forest site recognized by Schnur was that on which the total height of average dominant oaks was 40 feet at 50 years of age, while the poorest recognized by Meyer for ponderosa pine was 40 feet at 100 years. Both the upland oaks and the ponderosa pine on these marginally forest sites show maturity by flattish, rather than pointed, crowns at approximately 50 feet in height. Thus, some foresters, too, have recognized stands of oak and pine on sites poorer for tree growth than these, as something less than sites for commercial forestry.

The term "savannah site" seems most applicable to this segment of the environmental gradient between obviously grassland site and obviously forest site. This is with full recognition that a savannah site may now be occupied by a continuous cover of woody plants better referred to as a thicket than a forest, while a forest site may be occupied by a savannah type better referred to as an understocked forest type.

Nonarable sites on which savannah is climax can in many cases provide some incidental income from tree products; but the best management of grazing on such a site will inevitably conflict in some degree with greatest production of forest products. In any case, woody cover on savannah sites can produce only trees with little height or clear bole at maturity, and usually with limbs persistent to within a few feet of the ground.

Regrettably, the western limits of the forests of eastern United States are commonly drawn near the eastern edges of open grassland and near the western limits of natural tree growth of any kind. Thus much land has come to be known as forest land, and forest resource inventory data include great acreages of savannah sites. The nonarable acreage of such sites may now have a nearly continuous canopy of woody plants and in many ways may resemble second-growth forest. But, a savannah site produces only scrubby timber, of doubtful value because of climatic or edaphic limitations. Such nonarable sites where restored to normal savannah cover provide excellent natural pasturage with no loss in watershed values. The term range land would seem more appropriate than

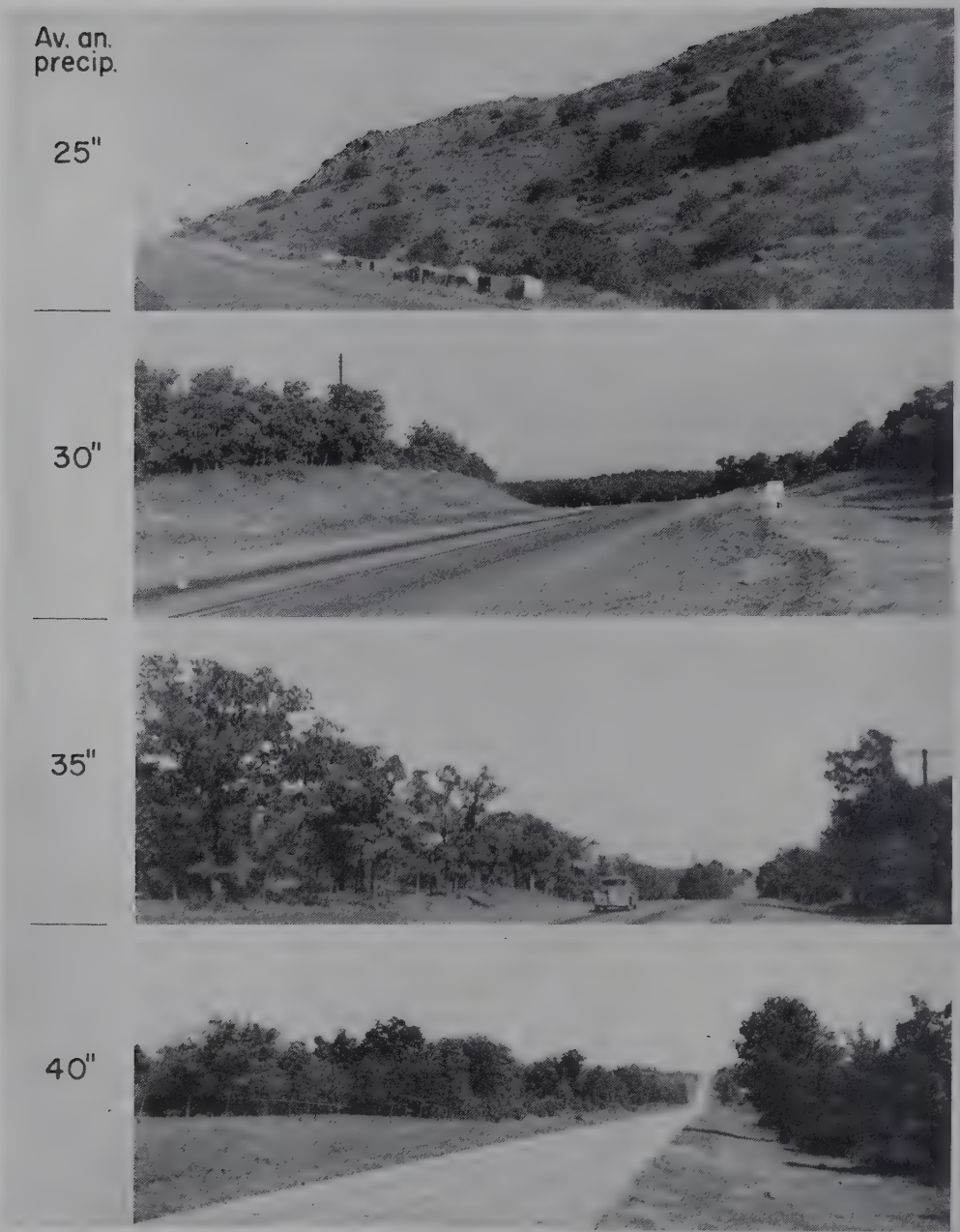
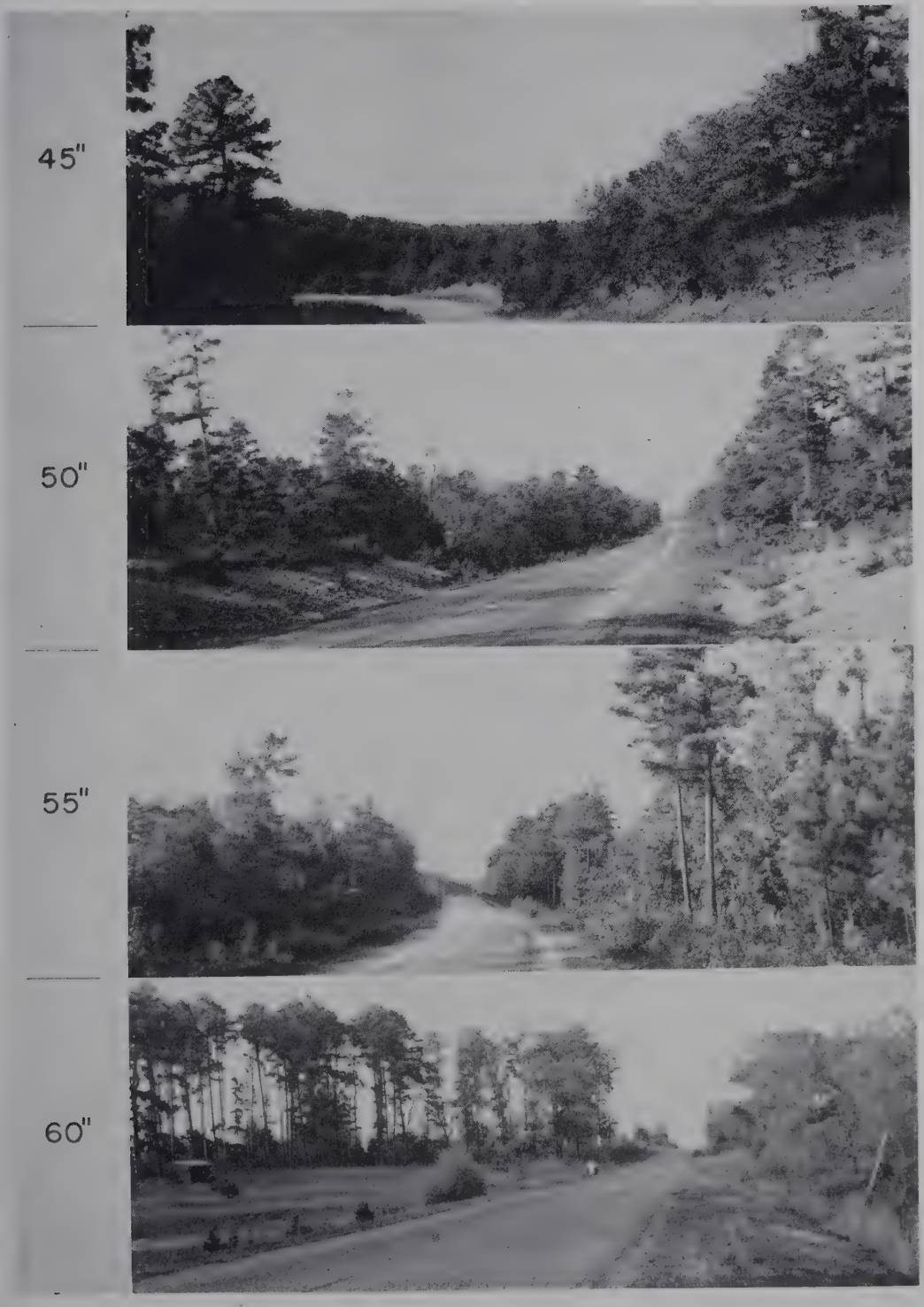


FIG. 1 inc. page opposite. Pictorial transect across the isohyets at the 34th North Parallel from the 100th Meridian 300 miles eastward. Photos are at five-inch increments in average annual precipitation from 25" to 60" on S. & W. exposures with noncalcareous deep, rocky or sandy soils. Tallest mature trees indicate site potentials. Lower canopy levels reflect deterioration of savannah to thicket under grazing (30" to 40" isohyet), and second-growth forest (50" to 60" isohyet).


45"
50"
55"
60"

forest land for the nonarable portions of the area of savannah climax (Dyksterhuis 1952).

The boundary between savannah site and forest site, or grassland site, admittedly is difficult to map; but it may be simpler than mapping a presumed boundary between forest site and grassland site where in reality miles of savannah site intervene. A series of photographs can illustrate and aid in resolving such a problem.

Pictures were taken along the 34th North Parallel from the 100th Meridian, eastward 300 miles. They provide a series of views for comparison of the native vegetation showing effects of five-inch increments in average annual precipitation from the 25-inch isohyet in southwestern Oklahoma to the 60-inch isohyet in southwestern Arkansas. In each photo a section of standard width, hard-surfaced highway is included for perspective in portraying the greater height of dominant trees with each five-inch increment in average annual precipitation. All photos were taken within 30 miles of the 34th parallel, between October 4 and 15, 1948. All photos are of south and west exposures having deep non-calcareous stony or sandy soils.

In Figure 1 the greater height of the tallest trees in successive pictures is regarded as indicative of the capability of the eight sites for timber production. Dominant trees having flattish, rather than pointed, crowns may be assumed to have reached maximum height for the site. Most of the eight stands show a nearly continuous level of canopies below the height of the scattered tall trees. From the 30 to 40-inch isohyet, post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*) are universal on uncleared, noncalcareous uplands but there is little hickory (*Hicoria spp.*). From the 40 to 45-inch isohyet hickories are constantly associated with the oaks on these uplands. From the 45-inch isohyet to the 60-inch isohyet on these uplands there is also shortleaf pine (*Pinus echinata*), southern red oak (*Q. falcata*), American sweetgum (*Liquidamber styraciflua*) and Black tupelo (*Nyssa sylvatica*).

The photo from the 25-inch isohyet portrays grasses, shrubs, and two low globe-shaped oak trees. The landscape is readily classified as a grassland site, probably with some invasion or increase of woody plants because of grazing. Photos at the 30, 35, and 40-inch isohyets show a second level of trees, below the height of the dominants, composed of tree growth subsequent to settlement and some 50 years or more of close grazing by domestic livestock. The landscapes are readily classified as savannah sites now supporting oak thickets. The photos at the 50, 55, and 60-inch isohyets had evidence of logging. The older trees showed 10 feet or more of clear bole. The lower level of trees here may properly be referred to as forest second-growth and the landscapes are readily classified as forest sites.

The foregoing leaves an area between the 40 and 50-inch isohyets where classification as either forest site or savannah site may be questionable. Since classification as savannah at 40 inches of precipitation and as forest at 50 inches of precipitation was not difficult at this latitude on these soils, it was arbitrarily decided that the line between savannah and forest sites could best be drawn near the 45-inch isohyet. The photo from this isohyet shows a mature dominant conifer on the left and a veteran hardwood on the right, each perhaps with enough clear bole to indicate forest site of the lowest site index for lumbering. But there also is evidence of a savannah condition that has deteriorated to a thicket-like growth of young hardwoods in consequence of grazing and less fuel for fires.

Interpretive groupings of soil units mapped in standard soil survey procedures present many opportunities to employ the savannah concept. Soil mapping units must usually be grouped in different ways to best serve different classes of users. In the five Northern Plains States the Soil Conservation Service has long used such a grouping for range users. Included among groups of range soils is a savannah group of soils. Savannah soils in grassland climates characteristically have much loose large rock, often with a fine-textured layer at considerable depth. By transfer of experience, both conditions are more readily deduced from presence and form of mature trees than from the limited number of soil profiles that can be exposed. The *Savannah* group of range soils in the Northern Great Plains is currently described as follows: ". . . uplands on which grass cover with isolated trees is normal (climax). This site is common at margins of forest climates but it also occurs deep in grassland climates if soil profile conditions especially favor storage of soil moisture. Soils with high intake at the surface and a slowly permeable layer several feet below may normally produce savannah cover even though in grassland climate. Also, in some cases reduced exposure to sun and wind as on north slopes, resulting in more economical use of moisture, may produce this site in generally grassland climate. Bedrock near the surface is not characteristic as on the Very Shallow soil-group. Heavy grazing and fire prevention have caused some savannah sites to be occupied by woodlands with 40 percent or more canopy of stunted trees and

brush but these are to be regarded as range sites rather than forest sites. Likewise, deteriorated open grasslands may be invaded by savannah types but these are not therefore to be regarded as savannah sites."

It will be noted that in the above description savannah *site* is sharply distinguished from savannah *type*. Thus, the description of the *Very Shallow* group of range soils states: ". . . Areas where few roots can penetrate deeper than 10 inches. Exposure of bedrock is characteristic but joints develop deep soil pockets. Joints are usually marked by tall grasses, shrubs, or stunted trees." This description recognizes that scattered trees may occur on generally very shallow delineations, but the soil-group is distinguished from the savannah soil-group. Relations between groups of Ozark soils, from very shallow to deep, and site index for native trees have been reported by Ray and Lawson (1955).

Conclusions

Effective use of the savannah concept requires recognition of (1) gradation of vegetation along environmental gradients as normal, and (2) abrupt boundaries between grassland and forest as unusual, ordinarily due to great difference in physical environment within a short distance. With increased understanding of natural vegetation as a continuum, the savannah concept should gain acceptance in explanation of cover types along environmental gradients between clearly forest climate and clearly grassland climate.

Use of the savannah concept has unquestionably been hampered by failure to distinguish between savannah *sites* and savannah *types*. A savannah type should be regarded as normal, or climax, only on a savannah site. But, savannah types of cover now occupy many other sites. Under prolonged close grazing and with absence of fire, which may be a result of close grazing, savannah sites tend to develop a continuous canopy of woody plants. In this condition they are sometimes mistakenly classified as forest land.

It is common to find savannah sites with cover deteriorated by grazing and, therefore, with spaces between veteran trees filled in with trees of younger age classes and shrubs. By observing the form and height of mature native dominant trees that attain greatest height in the site, and antedate settlement, such stands may be classified as occupying either forest or savannah sites. On forest sites the mature dominant trees will be tall with considerable clear length, while on savannah sites the mature dominants will be short generally less than 50 feet tall, with heavy branches persistent to within a few feet of the ground. Percent of ground cover by canopies of trees of all ages, and numbers of stems per acre, are of no help in distinguishing forest sites from savannah sites. Natural grasslands deteriorated by grazing are commonly invaded by scattered dwarfed trees and may now have a savannah type of cover but if the fact of invasion since settlement can be established, the site is to be regarded as grassland rather than savannah site.

Excluding instances of scattered trees rooted in joints of bedrock at or near the surface, the following are the more common examples of savannah types:

1) On forest sites within forest climate (anthropogenic savannah)
2) On savannah sites within forest climate (edaphic savannah)
3) On grassland sites within forest climate (anthropogenic savannah)
4) On forest sites within savannah climate (anthropogenic savannah)
5) On savannah sites within savannah climate (climatic savannah)
6) On grassland sites within savannah climate (anthropogenic savannah)
7) On forest sites within grassland climate (anthropogenic savannah)
8) On savannah sites within grassland climate (edaphic savannah)
9) On grassland sites within grassland climate (anthropogenic savannah)
10) On savannah sites within desert climate (edaphic savannah)

Among the foregoing conditions under which the savannah type of cover may be encountered, the type is normal and indicative of physical environment only in instances numbered 2), 5), 8), and 10). In number 5) savannah may be expected on normal soils; in number 2) on shallow or very fine-textured soils, and in numbers 8) and 10) on deep soils with unusually great infiltration and retention of moisture within the tree-root zone. In the other six instances of savannah types the scattered trees indicate disturbance of natural cover rather than factors of the physical environment.

Abundant tree reproduction will usually indicate a need for corrective measures in instances numbered 2), 3), 5), 6), 8), 9), and 10). Conversely, absence of tree reproduction in cases numbered 1), 4), and 7) will usually indicate a need for corrective measures. The foregoing should suggest different areas as of primary con-

cern to rangemen and foresters, rather than conflicting interests.

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CYCLIC FLUCTUATIONS OF POPULATION DENSITY INTRINSIC TO THE HOST-PARASITE SYSTEM*

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INTRODUCTION

The cyclic fluctuations of animal population caused by the interaction between prey and predator or host and parasite have long been predicted mathematically by Lotka, Volterra and Nicholson and Bailey, and experimental work to verify this mathematical postulate has been done by Gause (1934, 1935), DeBach and Smith (1941) and the present author (Utida 1950, 1955). In experimental population of protozoans and mites, Gause demonstrated so-called relaxation oscillations and was able to produce cyclic fluctuations of the classic type only when periodic "immigrations" of prey were made. The experiment of DeBach and Smith, using the pupae of the house fly and its hymenopterous parasite, was devised very ingeniously, the host's power of increase being fixed at a constant value; the resulting fluctuations of population density obeyed the mathematical model of Nicholson and Bailey. Unfortunately, however, the experiment terminated at the seventh generation, before one complete wave of population fluctuation had been shown. The present author attempted to find cyclic fluctuations in the interacting population of the azuki bean weevil, *Callosobruchus chinensis,* and its larval parasite *Neocatolaccus mamezophagus,* avoiding artifical "immigrations" and without arbitrary limitation of the host's reproductive power, but no clear fluctuation having a definite amplitude and wave length could be found (Utida 1950). Thus experimental demonstration of theoretical cycles is not ordinarily achieved, and there remain many doubtful points in the results of the experiments. An exception may be made for some more recent work of the present author (Utida 1955), which gives a clear demonstration of cyclic fluctuations of population density, covering 25 generations of population interaction between the azuki bean weevil and the larval parasite *Heterospilus prosopidis* (Hymenoptera, Braconidae).

The present paper is a continuation of the previous work. Three of the six experimental populations were continued from the 25th generation until long after the termination of the experiments described in the previous paper. The main problem of the present paper is whether the populations continue to fluctuate with the same wave

* Contribution from the Entomological Laboratory, Kyoto University, No. 261.

length and amplitude even after very many generations.

Methods

Here only a brief outline of the method is given, since the full account has already been given elsewhere (Utida 1955). The mixed populations of the azuki bean weevil and its larval parasite *Heterospilus prosopidis* were run in Petri dishes 1.8 cm high and 8.5 cm in diameter. The temperature and the relative humidity were maintained constant at 30°C and 75 per cent respectively. Ten grams of azuki beans (the seed of *Phaseolus angularis*), with water content of about 15 per cent, were placed in each Petri dish every ten days to serve as food for the weevils.

Three mixed populations, called populations A, C, and E, were run in the Petri dishes, starting with different combinations of initial densities of host and parasite, *viz.* 64 weevils and 8 wasps, 8 weevils and 8 wasps, and 512 weevils and 128 wasps, respectively. The number of each sex of dead and living adults of both species was counted at ten-day intervals. Living adults were lightly anesthetized with ether, counted, and then put back in the culture dish. At each census a new supply of beans was provided and the most ruined part of the food was removed to another dish, where counts were continued until 20 days after the separation.

Results

The results of the counts of both host and parasite populations show that the numbers of living and of dead adults increase and decrease in turn, with a period of about 20 days. This is apparently caused by the emergence and death of adults belonging to each generation. When the generations do not overlap, as in the present case, the number of individuals emerging in each generation is a better index to population fluctuation than is the number of living or dead animals observed at the times of census. To eliminate the intra-generational population fluctuation, the number of emerging individuals belonging to two consecutive counts should be summed, for the double census period of 20 days closely approximates the time required for a generation of hosts. In this way the total numbers of hosts and parasites that emerged in each generation can be obtained, and these values are treated as the population densities of each generation.

The changes of density in the host and parasite populations are shown in Figures 1 and 2, including the data for the first 25 generations as previously reported (Utida 1955).

Fluctuations of population density can be seen for both host and parasite in each of the three experimental populations. In population A, the densities of host and parasite fluctuated rhythmically and reciprocally up to the 112th generation, when the population was accidentally destroyed. Population C was also destroyed by careless handling at the 47th generation. By contrast, although population E was not subjected to accidental disturbance, complete extinction of the host population was observed as a consequence of eruptive increase of parasite density.

In each of these three experimental populations, it is evident that in the initial stages in their history the densities of host and parasite rose and fell reciprocally, as described in the previous paper (Utida 1955); with the progress of the experiment, however, the fluctuations diminished in violence and approached a relatively stable level or steady state. In other words, the oscillations of density are damped. This trend of convergence was not found in the data described in the previous paper, for the 25 generations provided too short a time in which to detect it. The damping is now easily seen to have occurred before the 25th generation in population C, but it was disregarded in the previous paper for lack of confirmation.

Damping of the oscillations is especially well illustrated when the densities of host and parasite in each successive generation are plotted against each other, as in Figures 3 and 4. The cyclic fluctuations of density are repeated one or several times with gradually diminishing amplitude, and finally change to a steady state, after which the cycles, if present, are too small to be seen on the graphs. The final level attained is the same as the singular point of Gause (1934).

A very interesting fact is that in the course of many generations the damping of fluctuations occurs repeatedly, as seen in Figures 1 and 2. After the populations passed through several tens of generations in a state of steady density, relatively violent oscillations suddenly recurred and were damped in their turn. In population A, the first series of damped fluctuations attained its steady state at about the 30th generation, after which the fluctuations increased in amplitude before approaching the next phase of damping. This second phase was relatively protracted and was not broken until after the 80th generation; a third phase of damping ensued. In population C two phases of damped fluctuations can be seen, the division between them coming at the 20th generation. In population E as many as 70 generations elapsed before a second phase began; the second phase ended when the hosts died out at the 82nd generation.

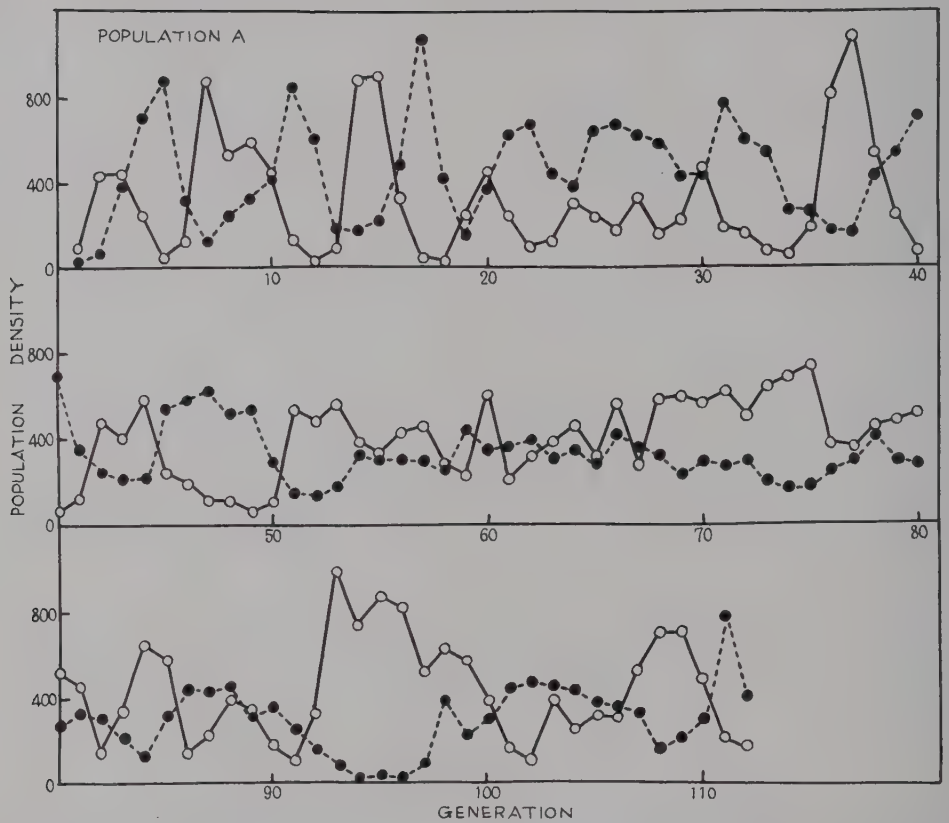

FIG. 1. Fluctuation of population density from generation to generation in population A. Host population: ——o——, Parasite population: -----●-----

Although the host and parasite densities are essentially constant during any one phase of damping, a long-term trend seems to be superimposed on the damping cycle itself. That is, in each successive phase of damping the host populations seem to rise and the parasite populations seem to fall. This tendency is also clearly shown in Figures 3 and 4. In the first phase of damping the singular points (representing steady densities) are situated near the ordinate, while in the second or third cycle of damped oscillations they tend to move downward toward the abscissa.

When the more violent fluctuations are smoothed by moving averages of seven consecutive points, the long-term trend of population density is obtained, as shown in Figure 5. Seven consecutive points were taken because the mean length of the short-period fluctuations (obtained by statistical methods) was about seven generations, as mentioned in the previous paper (Utida 1955). In each experimental population the host density increases steadily while the parasite density decreases. Accordingly, the incidence of parasitism (the numerical ratio of parasite to host) decreases with the progress of the generations. Since the long-term trends were the same in the three experimental mixtures, despite the fact that the initial preparations of parasite and host were different, it would seem to follow that the equilibrium proportions are not given by the singular point of any one wave or of any one phase of damping, but by the mean proportions throughout the entire population history.

DISCUSSION

Some important points to discuss here are deduced from the results obtained.

The first point is whether the fluctuation of population density is intrinsic to the system of host-parasite interaction. Since internal oscilla-

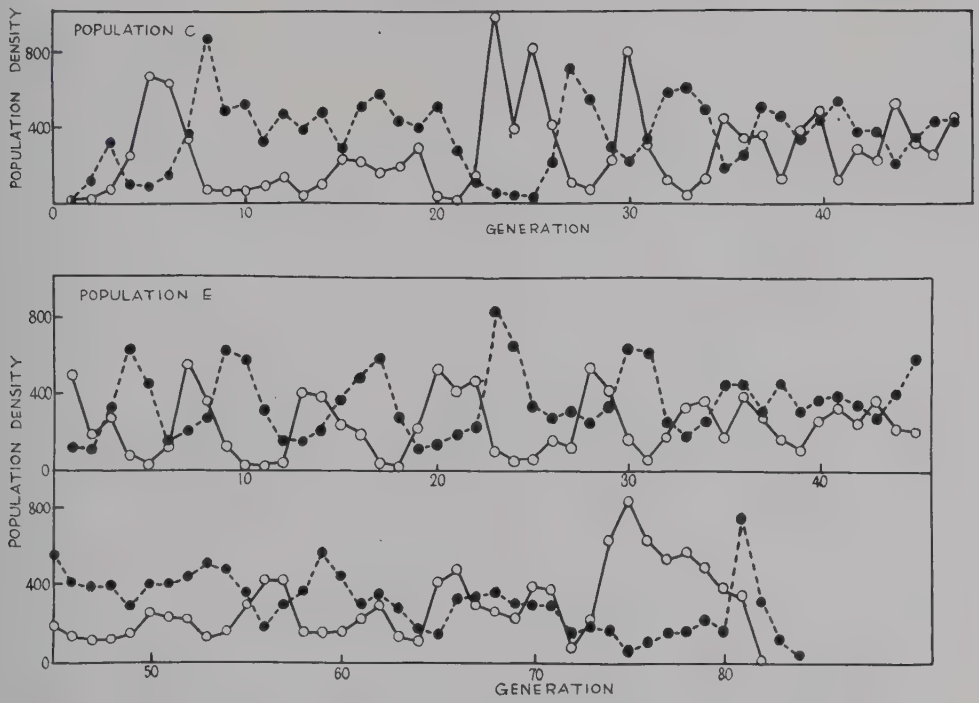

FIG. 2. Fluctuation of population density from generation to generation. Upper: population C, Lower: population E. Host population: ——o——, Parasite population: -----●-----

tions have been clearly shown in the author's previous paper (Utida 1955), as well as in the present paper, their existence no longer affords any room for doubt. The relation between the cyclic fluctuations of host and parasite populations can be clearly understood by Gause's method of graphic representation, as shown in Figures 3 and 4. This representation of the interaction does not show the usual form of a circle or an ellipse, but the irregular form of an obliquely squashed polygon, which represents the delayed effect of the parasite upon the host population. One can conclude that lag effects are common in host-parasite or prey-predator interactions, as emphasized by Varley (1953).

Next, it must be remarked as an important finding that the fluctuation obtained is a damped one, decreasing in amplitude with the progress of generations, and finally converging to the level of steady density, the singular point of Gause (1934). It is noteworthy that the fluctuation obtained does not belong to the classical type of fluctuation in the mathematical theory of Lotka and Volterra.

Nicholson (1933) considered that this type of damped fluctuation should be found when a parasite attacks other species of host in addition to the host under consideration. It is also to be expected in two-species systems where the host population is closely controlled by the effect of its own density, as pointed out by the present author (Utida 1955). Experimentally, a similar finding was made in the interaction between *Paramecium* and *Schizosaccharomyces* (Gause 1934, 1935), but the problem requires further investigation. In the writer's opinion, the damped fluctuation is more important than the "conservative" or classical type of fluctuation, for the former type is generally characteristic when, as is usual, the host population is controlled both by attack of its parasite and by the influence of its own density.

Returning to the curves of Figures 1 and 2, we note that there is repetition of the cycle of damping when the interaction is observed for very many generations. There were three repetitions in population A, two in population C, and nearly two in population E.

Such cyclic repetitions of shorter-term cycles must be given special attention, for this may prove to be one of the most important points in population dynamics. In the present state of our knowledge, however, we cannot give any plausible ex-

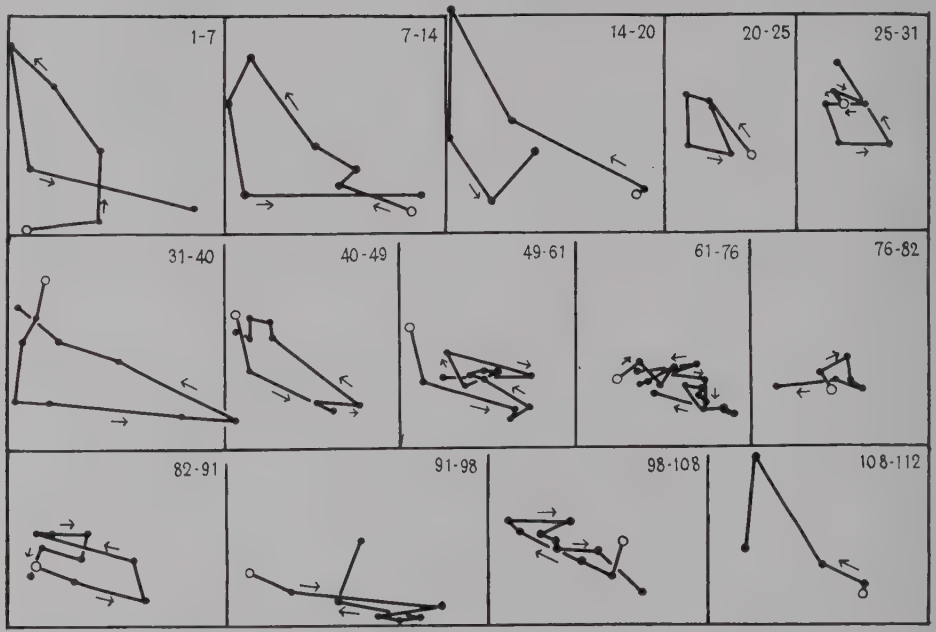

FIG. 3. Graphic representation of cyclic interaction between host and parasite populations in population A. Density of host population on abscissa, density of parasite population on ordinate. Each figure shows a complete cycle of fluctuation which starts and finishes at the generations whose numbers are given in the corner of each figure.

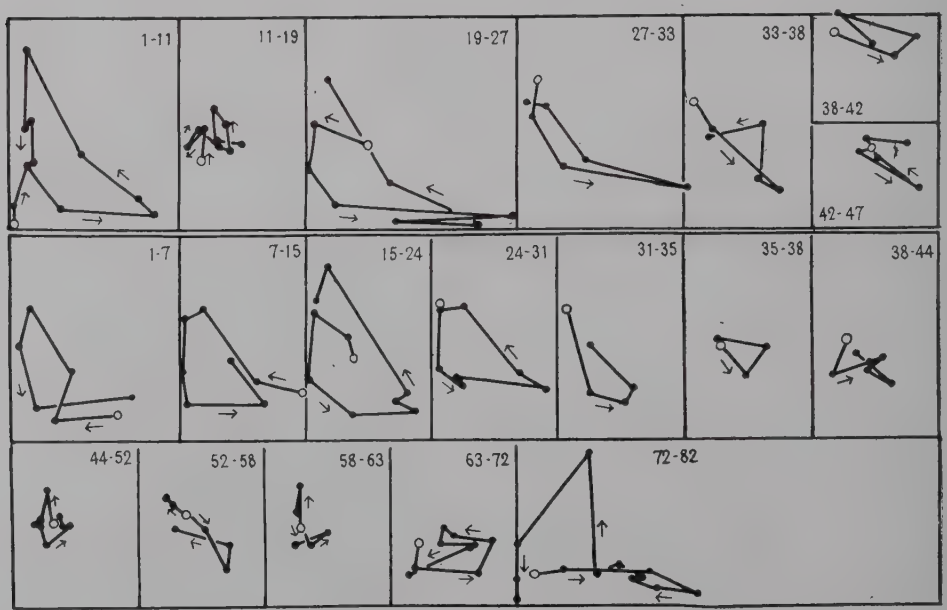

FIG. 4. Graphic representation of cyclic interaction between host and parasite populations. Upper figure: Population C. Lower figure: Population E.

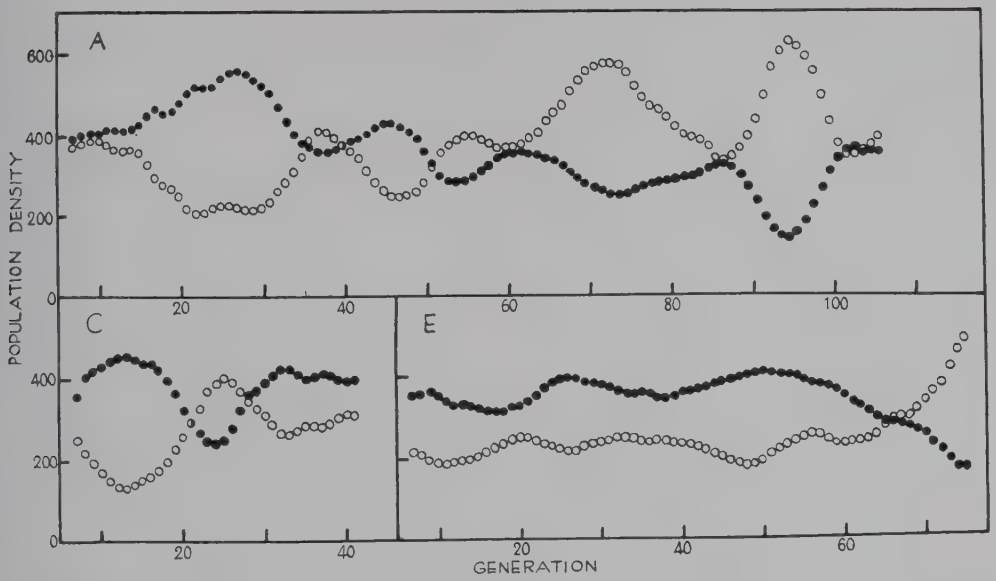

FIG. 5. Long-term trend of population density. The plot is the result of smoothing by moving averages of seven consecutive points. Host population: o, Parasite population: •

planation of the stimulus that forced the populations into a new phase of damped oscillations after they had previously attained steady states. In each experimental population the relative proportions of host and parasite populations changed with the onset of each successive phase of damped fluctuations. The change can be seen not only in the level at which the steady density of host and parasite is maintained, but in the relative form of the cyclic fluctuation, as clearly shown in Figures 3 and 4. In other words, the average percentage of parasitism decreases, as does the effect of the host's density on the parasite's power to keep the host population in check.

On the basis of mathematical analysis described in the previous paper (Utida 1955), it is considered that these changes in the values and form of the host-parasite interaction should reflect changes in the biotic potential and in the environmental resistance of host or parasite. In particular, the change in the biotic potential of the parasite may be the principal factor responsible. When we plot on a graph the relation between the density of the adult population and its rate of reproduction, as given by the ratio between the sizes of successive generations, the values obtained for the host species fall on a single curve; this is the curve for the equation describing the effect of population density on rate of reproduction:

$$R = \frac{N_2}{N_1} = 2\left(\frac{1}{b + c\,N_1} - \sigma\right) \qquad (1)$$

where N_1 and N_2 are the population densities in two consecutive generations, R is the rate of reproduction, and b, c, and σ are specific constants (Fujita and Utida 1953). On the other hand, the values for the parasite's potential are scattered and cannot be described by a simple equation. The relation is not improved when the parasite's adult density, N_1, is made more constant by taking the value P_n / h_{n+1} (which reduces the parasite density to a constant proportion of hosts available for parasitisation). However, the plots obtained accord well with the above equation for the comparatively short span of the first 25 generations (Utida 1955).

This contradiction between short-term and long-term results can be resolved by breaking the graphs into several parts, each corresponding to a separate phase of damped oscillation. The separate graphs then yield straight lines, each of which is precisely described by the above equation, but with different numerical values for the constants, as shown in Table I. In particular, the constant b, the characteristic coefficient of the biotic potential, varies widely, while the constant c, an index of the environmental resistance, remains relatively

stable. This result supports the suggestion that the changes in value and form of the cyclic interaction are mainly due to changes in the parasite's biotic potential.

TABLE I. Values of constants b and c, representing parameters of the parasite population. Successive phases of damped oscillation are treated separately in calculating the constants from equation (1)

Population	Range of generations	Numerical Values of Constants	
		b	c
A	1 - 31	0.35	0.162
	32 - 82	0.40	0.162
	83 - 112	0.45	0.153
C	1 - 19	0.30	0.213
	20 - 47	0.40	0.141
E	1 - 38	0.38	0.231
	39 - 62	....	.....
	63 - 82	0.30	0.231

The long-term trend of population change mentioned above can also be clearly represented by smoothing the data statistically; Figure 5 is the result of smoothing by moving averages of seven consecutive points. It reveals a rising trend in the host population, a declining trend in the parasite population, and also several slow undulations. The rising or declining trend is most conspicuous in population A, which was followed for the longest time, and is not at all clear during the short history of population C.

A similar tendency to long-term population fluctuation can be seen in the interaction between the azuki bean weevil and another larval parasite, *Neocatolaccus mamezophagus* (Utida 1950), when the data are similarly smoothed. Figure 6 is the result of this smoothing. In one of the two experimental populations the declining trend of the parasite population is particularly distinct. This additional example reinforces the soundness of the results reported here.

The problem remains to study further the stimulus that induces such changes in host and parasite populations. Natural selection provides the readiest explanation. That is, it may be presumed that the game of hide-and-seek between host and parasite intensifies the host's ability to conceal itself, or otherwise to avoid attack by the parasite. This selection pressure will be operative at all times, but should be most potent when the host population is in the trough of a cycle while the parasite population is at a peak. Increased success in concealment on the part of the host should

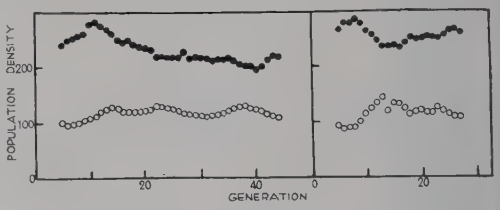

FIG. 6. Long-term trend of population density observed in the interaction between the azuki bean weevil and another larval parasite, *Neocatolaccus mamezophagus*. Host population: o, Parasite population: •

then cause the decline of the parasite's population. On the other hand, the change in the biotic potential of the parasite may be the primary cause of the parasite's own decrease, if some ecological advantage is linked to a lowered reproductive ability. In the present state of our knowledge we cannot judge which of the two explanations is more plausible.

SUMMARY

Under experimentally controlled conditions, populations of the azuki bean weevil, *Callosobruchus chinensis*, were subjected to attack by the wasp *Heterospilus prosopidis*, which parasitizes the weevil's larvae. The interacting populations were maintained in the laboratory for as many as 112 successive generations.

Violent reciprocal fluctuations of population density were observed, the parasite's fluctuations being somewhat displaced in phase in relation to those of the host. The oscillations were gradually damped in amplitude, but episodes of renewed oscillation followed by damping were found to occur repeatedly.

The value of Gause's singular point, representing the steady proportion of parasite to host population, was different for each successive series of damped oscillations: that is, a long-term trend was superimposed on the cycle, such that the host population gradually increased and the parasite population gradually declined. This trend is inferred to be the result of a fall in the parasite's biotic potential.

ACKNOWLEDGMENTS

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POPULATION STUDIES OF THE SLAVE-MAKING ANT *LEPTOTHORAX DULOTICUS* AND ITS SLAVE, *LEPTOTHORAX CURVISPINOSUS*[1]

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Introduction

In 1935 Laurence Wesson, working in Jackson County, Ohio, found a new slave-making ant which he named *Leptothorax duloticus*. These were enslaving ants of their own genus—*L. curvispinosus* Mayr and *L. longispinosus* Roger. Wesson collected alive three of the four mixed colonies which he saw and was unusually successful in maintaining and observing them. In two papers (Wesson 1937, 1940) he described workers, males and females and recorded his observations of three raids made by colonies in the laboratory. No further accounts of finding *L. duloticus* have been published. (Creighton, in his 1950 revision of the ants of North America, lists its range as Ohio and Illinois, but he and others contacted were unable to trace any knowledge of the Illinois record.) In 1954 the writer found it in Livingston County, Michigan, at the Edwin S. George Reserve. Shortly after *L. duloticus* was discovered at the Reserve, Paul Kannowski informed me that he had taken it near Ann Arbor, Washtenaw County, Michigan.

It may be that *L. duloticus* is a very rare and local ant, or it may be that it has been overlooked because it is so similar in structure and color to the yellow *L. curvispinosus,* which it usually enslaves. Under the microscope the stout, widespread spines, broad postpetiole and dusky tinge to the yellow color distinguish it readily, but these differences are difficult to observe in the field.

This paper concerns population studies of unparasitized *L. curvispinosus* colonies and of mixed colonies of *L. duloticus* and *L. curvispinosus* to show their interrelationships and to contrast development of brood of the species during the summer months of 1955 at the Edwin S. George Reserve. For two reasons the study is restricted to colonies living in acorns: these are easy to collect complete (except for workers which are out foraging) and so are favorable material for population studies, and at the Reserve, *L. duloticus* has, so far, been found mainly in acorns. The host species, *L. curvispinosus,* is versatile in its choice of nesting sites. Colonies may be found under the bark of standing trees, in the more solid parts of fallen logs, in all types of hollow twigs lying on the ground, in hickory nuts and oak galls and, most abundantly, in acorns. That *L. duloticus* is not confined to those colonies living in acorns is attested to by the fact that Wesson found his in an oak gall and in cavities of sticks lying on the ground.

The Edwin S. George Reserve, in southern Michigan, consists of two square miles of rolling country rich in a surprising variety of habitats for ants. Acorn-dwelling *L. curvispinosus* colonies are common in the extensive oak-hickory woods, especially in the more open woods and at the edges of fields. Acorns may be either black or white oak (usually the much more common black), but the condition of the ground where they lie is important. It must not be covered by a heavy leaf layer, for this encourages the development of mold. Favorable places are areas of scant leaves, many small twigs, a sparse stand of

[1] The work was assisted by a grant from the Edwin S. George Reserve scholarship fund. Facilities of the Reserve were made available by Dr. T. H. Hubbell, Acting Director, and Dr. Irving J. Cantrall, Curator of the Reserve.

Canada blue grass or the small grass-like wood sedge, *Carex pensylvanica* Lam., and scattered bracken and blueberry or young oak and hickory trees. A gentle slope provides good drainage which is important. In drier places, occupied acorns may be partly buried under leaves or twigs while in more moist spots they are lying on top. Acorns suitable for ant occupation are often confined to surprisingly small areas. The best collecting sites are on slopes of rather high, dry woods where leaves are not abundant, and in narrow strips between woods and fields where the ground is neither too moist and leaf-covered nor too dry.

The condition of the acorn is also important. It must not be too new (hard or filled with acorn seed) nor too old (brittle or cracked). It must not be moldy, too dry, or too moist. Ants take over acorns first occupied by Curculionid beetles of the genus *Balaninus*. These beetle larvae eat out all or most of the seeds and then leave by way of circular openings, which are often through the cup or near it, seldom near the pointed end. They may be used by the ants just as they are, or they may be made smaller by the addition of rings of carton. Inside, the acorn is often clean and hollow, but it may have a core of remaining acorn seed or an accumulation of larvae droppings. Occupied acorns seem to be two or more years old, and often they have been inhabited by other larvae which have succeeded the Curculionids and finished eating the contents.

L. duloticus was, of course, found only where *L. curvispinosus* was abundant, but in many parts of the Reserve there were no *duloticus* through *curvispinosus* were common. Even where *duloticus* colonies were found, they were strangely restricted, being almost always in groups. Often *curvispinosus* only a short distance away would be unparasitized. During collecting, acorn colonies from beneath different trees were sometimes kept separate. Along one strip of woods border, *duloticus* colonies were found beneath 7 trees but not beneath 4 others although locations were almost touching. Again, in the woods 13 *curvispinosus* colonies beneath one tree were unparasitized while under another nearby each of 4 colonies collected had *duloticus* guests.

No *duloticus* raids were seen although a series of acorn nests were staked and observed frequently. Therefore, information concerning relationships is limited to that obtained by numerous collections of colonies.

Methods

Collecting was done by putting acorns containing colonies into small bottles to be taken to the laboratory for killing and counting. Usually unparasitized *L. curvispinosus* colonies could not be distinguished from mixed colonies in the field, so large numbers of *curvispinosus* had to be collected in order to get sufficient numbers of *duloticus*. All unparasitized *curvispinosus,* as well as the mixed colonies, were counted, thus giving a population study of *curvispinosus* in addition to the one of *duloticus* and showing the contrast in development of brood.

In all, 525 collections of *L. curvispinosus* and 270 collections of *L. duloticus* (with their slaves) were made. The first were made in August of 1954, soon after *duloticus* was discovered, but for purposes of showing development of brood, assembling of data was started in June, 1955. Lists of populations cannot be given because of the space involved, but summaries of numbers and of development of brood are given for *L. curvispinosus* on Figure 1 and Table I and for *L. duloticus* on Figures 2 and 3.

Table I. Percentage of colonies of *Leptothorax curvispinosus* producing sexual forms, and the mean number of males and females in these colonies. Pupae and adults are not distinguished

Date	Colonies collected	Colonies with winged ants	Percent of colonies with winged ants	Colonies Producing Winged Ants		
				Males per colony	Females per colony	Total winged ants per colony
June 13-30...	89	41	46.1%	8.0	4.8	12.8
July 1-10...	82	46	56.1%	4.2	5.0	9.3
July 11-20...	42	12	28.6%	6.6	1.5	8.1
July 21-31...	91	3	3.3%	1.7	0.7	2.3
Aug. 1-10...	41	2	4.9%	1.5	...	1.5
Aug. 11-20...	48	1	2.1%	1.0	...	1.0

Leptothorax curvispinosus

Colonies Which Were Not Enslaved

Maturing of brood. When collections began on June 13 there were already worker, male and female pupae in the nests. Presumably these came from the over-wintered larvae and evidently all of the males and females had already pupated, because there were no male- or female-producing larvae present. There were worker larvae of all sizes, the smaller ones undoubtedly from spring-laid eggs. Eggs continued to be laid throughout the summer, and as a result worker larvae were constantly augmented. By June 18 some worker pupae were becoming yellow. The first callow workers were found June 21, but they did not become numerous and general in colonies until the first week of July. From then on throughout the summer callow workers were always present.

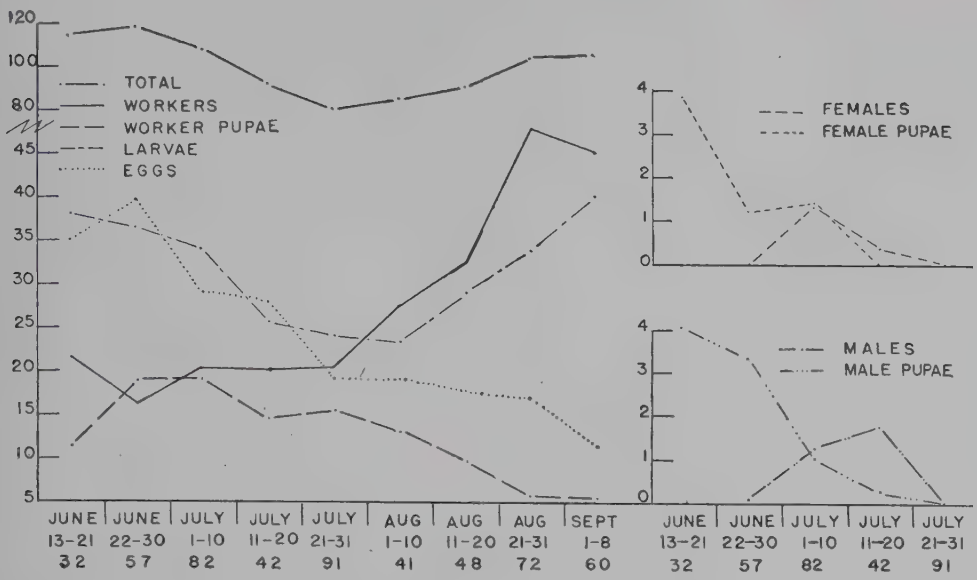

FIG. 1. Populations of colonies of the ant *Leptothorax curvispinosus* Mayr. Mean number of ants per colony is given at the left. Dates and numbers of collections are at the bottom.

The first 3 males were found on June 23, and 3 more were found June 29; but they, like the workers, were not numerous until the first week of July. Emergence was rapid during the first two weeks of July, but only 9 male pupae were found after that (on July 15, 18 and 22). Females emerged during a much more restricted period of time. The first adults were found July 3, and almost all had emerged by July 6 (one female pupa was found on July 7 and one on July 13). They were almost completely pigmented from the first and moved about quite actively in contrast to the males, which always looked pale and immature.

No flights were seen, but 4 winged females were taken at the laboratory lights on the night of July 7. Probably both males and females left the nest soon after they emerged, because the count of adult males and females never equaled that of male and female pupae. A few winged ants were still present in each of 6 nests on July 18, but after that only 2 adult females (July 22) and 3 adult males (August 3 and 15) were found. Major flights seem to have taken place between July 7 and July 18. Probably some females failed to fly and lost their wings in the nest, for multiple dealate females were more numerous in colonies after flights.

Populations. Figure 1 shows mean populations from June 13 to September 8. The peaks of total population came in late June when egg production was at its height, larvae were abundant and pupae from over-wintered larvae were becoming numerous, and again in late August when the worker population was built up from the summer brood. The proportionate numbers of workers, winged ants and brood varied markedly with the passing of the season. In June, eggs and larvae accounted for the greatest part of the population, and worker pupae were augmented by those of winged forms. At this time the worker population was at its lowest; evidently more and more over-wintered worker adults were becoming lost as they foraged, and only a few new workers had emerged from the pupal stage. During early July, males and females were conspicuous in many colonies, and eggs and larvae were less numerous. The lowest point in total population occurred just as flights were over and colonies had lost their males and females. During August there was an abrupt rise in newly emerged workers. By September almost all of the pupae had become workers and colonies were made up primarily of workers and larvae. Eggs and pupae were not over-wintered.

The largest number of workers found in an acorn was 113. This colony was taken at the end of the summer (August 25) when there was little brood. It had no pupae, 77 larvae and 34 eggs. The largest total population consisted of 491 individuals collected June 23, but two-thirds of these were eggs. The mean size of a colony

was 100.5 individuals. This is less than half the 235.0 average colony reported by A. E. Headley (1943) for *L. curvispinosus* colonies collected in northeastern Ohio. His were also acorn-dwelling colonies, so constricted living quarters could not account for the smaller Michigan populations. At the Reserve, most collections were made near to areas where *duloticus* is known to occur, so some of the populations may have been depleted by previous *duloticus* raids.

Production of males and females. Over-wintered larvae gave rise to all of the males and females. They had already pupated when collecting began in June, and pupae dwindled rapidly as adult males and females emerged in early July. Adults remained in the nest for only a short time and almost all had flown by the middle of July.

Table I and Figure 1 give a summary of males and females collected (pupae and adults). In June all were pupae, except for 6 males. Other records were both pupae and adults. During June and early July, about one-half the colonies collected contained winged ants (either pupae or adults). Flights presumably began about July 7, and Table I shows that in the July 11 to 20 period, numbers of colonies containing winged forms dropped considerably, but the number of winged ants in colonies which still contained them dropped very little. Evidently all had flown from some nests while other colonies had not yet had a major flight.

For a more accurate idea of the number of winged ants produced by this species, records were summarized from the time that pupae were most abundant to the time when adults had reached their peak and few had flown (June 13 to July 10). During this time about half the colonies contained winged ants—87 out of 171 collected. These 87 colonies had a mean per colony of 10.9 winged ants, 6.0 being males and 4.9 being females. The average worker population of the 87 collections was 23.6, giving one winged ant to every 2.2 workers. The 84 colonies not producing sexual forms had a mean of 15.2 workers per colony. The greatest number of winged ants in any one colony was 62. These were all females. The largest collection of males was 55 (with 2 females). Many colonies produced only one sex: 37 had only males, 25 had only females and 25 had both.

Queens. The large number of queenless colonies was puzzling. Of the 525 collections, 149 (35.2%) had no queens. This is similar to Headley's findings in his Ohio collections (1943). He found that 31.6% of his 38 colonies had no queens. The number of queenless colonies was greatest in early summer and declined as the season progressed: June, 38.2%; July 34.0%; August, 23.0%; September, 8.3%. Some queens may not have survived the winter or some may have been outside the acorn nest when collections were made. Another possibility is that a colony may sometimes occupy more than one acorn.

After flights some females must have stayed in the nest or were taken into other colonies. During June only 3 of 89 (3.4%) colonies had more than one queen. In July 3.7%, August 7.5% and September 10.0% had more than one. Most of the colonies with multiple queens had only 2, but a few had more, with one colony reaching the peak of 14 dealate females.

LEPTOTHORAX DULOTICUS AND ITS SLAVES

Distribution on the Reserve. L. duloticus was found in only a few places on the Reserve. Big Island and adjoining Duloticus Island (named for the *duloticus)* proved to be the best collecting grounds. These "islands" are oak- and hickory-covered knolls in the midst of an extensive larch (*Larix laricina* Koch)—posion sumac *(Rhus vernix* L.) swamp. Even here the species was restricted to the more open slopes where leaves did not accumulate. The other good collecting ground was along the abrupt edge of woods bordering a field which had once been cultivated. Two hundred and thirty-two of the 270 collections were made at these 3 places. The other 38 came from 7 other spots scattered over the Reserve. As not all parts of the Reserve were sampled, there may be other places where *duloticus* is present or even abundant. Means of populations of *L. duloticus* and its slaves are recorded in Figures 2 and 3.

Species enslaved. At the Reserve all *duloticus* colonies enslaved *L. curvispinosus* Mayr. In addition, a few acorns contained one or another of two additional enslaved species. These were *L. ambiguus* Emery in 7 collections and *L. longispinosus* Roger in 15. Usually *curvispinosus* lives in places slightly more moist than those inhabited by *ambiguus* and slightly drier than those occupied by *longispinosus.* All of the colonies made up of 3 species were found in the *curvispinosus* habitats. In their slave raids *duloticus* must have extended farther than usual into the fields to obtain *ambiguus* and into the more moist woods to obtain *longispinosus.* There were never many of the accessory slaves in any one colony. The 7 collections with *ambiguus* averaged 21 *ambiguus* workers, and the 15 collections of *longispinosus* averaged only 12 of

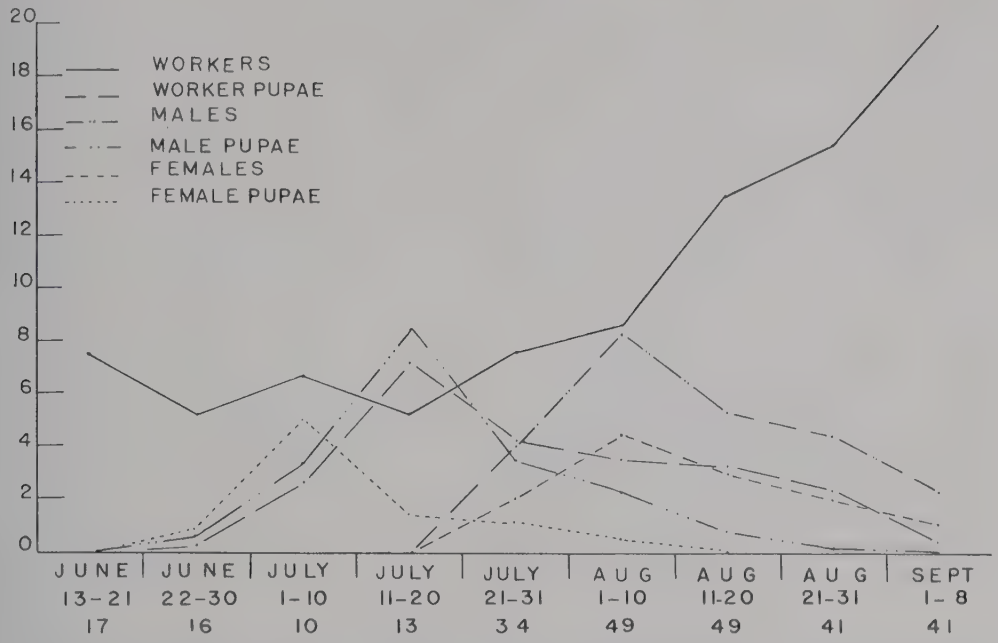

FIG. 2. Populations of colonies of the slave-making ant *Leptothorax duloticus* Wesson. Mean number of ants per colony is given at the left. Dates and numbers of collections are at the bottom.

these workers per colony. Pupae of *ambiguus* and *longispinosus* were never abundant and were not present at all in two-thirds of the colonies. In any records of totals, populations of *ambiguus* and *longispinosus* were included with those of *curvispinosus*.

Mixed colonies with *L. longispinosus* were quite conspicuous since the black workers contrasted sharply with the yellow *duloticus* and *curvispinosus*, but colonies containing *ambiguus* were not distinguished until they were put under a microscope, because their color was essentially the same as that of the two other species.

Development of brood. A study of brood was complicated by the fact that eggs and larvae of *duloticus* could not be distinguished from those of enslaved species. Presumably during the raiding season the number of slave larvae (and possible eggs) would be high and when raids ceased, the proportion of *duloticus* larvae and eggs would rise.

Wesson (1940) concluded that *duloticus* carried on its raids early in the summer. This makes it differ from such slave-making ants as *Formica subintegra* Emery and *Polyergus lucidus* Mayr which delay beginning their raids until mid-summer, when males and females are leaving the nest and worker populations have been augmented. Wesson said "workers begin scouting in the spring about the time that the eggs laid at the commencement of the season begin to hatch, and cease on the emergence of the brood in mid-summer." Wesson also stated that *duloticus* capture eggs and pupae as well as larvae. If this is true for the Michigan *duloticus*, then eggs and larvae would be mostly those of *curvispinosus* in early summer and predominantly those of *duloticus* later in the season. The egg population showed the following means for the approximately 10 day periods from June 13 to September 8: 30.6, 38.9, 52.0, 45.8, 39.0, 18.9, 12.7, 7.8, 3.6. The high in early July probably represents a maximum egg laying by *duloticus* females plus raided eggs, and the low in September indicates that no eggs were over-wintered.

Larvae had the following means for the same periods: 40.3, 41.3, 38.3, 31.0, 28.0, 18.6, 28.9, 32.6, 33.5. The high numbers in June probably denote vigorous raiding, while the drop to 18.6 in early August may show that raiding had ceased. If this is true, then the build-up of larvae to a mean of 33.5 in September would lead one to assume that *duloticus* larvae are overwintered. Unfortunately, no winter collections could be made.

From the middle of June to its end, some colo-

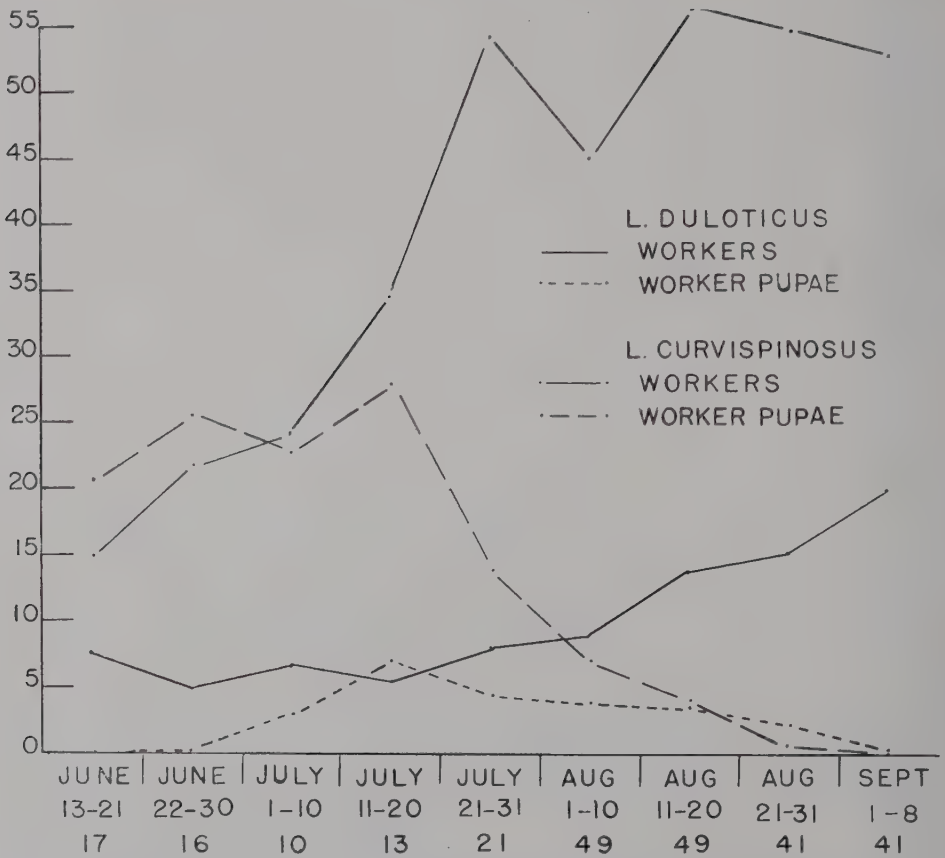

FIG. 3. Comparison of populations of workers and pupae of the slave-making ant, *Leptothorax duloticus* with captured workers and pupae of its slave, *L. curvispinosus*. Mean number of ants per colony is given at the left. Dates and numbers of collections are at the bottom.

nies had larvae which were larger than the usual worker larvae. These were presumably *duloticus* females. Worker and male larvae probably developed at the same rate since all began to pupate during the last week in June: the first male pupae were found June 26, the first worker pupae June 28 and the first female pupae June 29.

The first callow workers were found three weeks later (July 21), and after that colonies regularly had a few callows. Worker pupae reached their greatest abundance in mid-July and declined after that until only a few were present by the first of September.

Males and females matured at about the same rate as did workers. The first adult males were taken July 21 and the first females July 22. Males were almost fully pigmented when they emerged from the pupal stage—a gray which soon turned to black. Thus they were quite distinct in coloring from the whitish *curvispinosus* males. Females were a cream color which gradually turned to full yellow, darkening a bit on the head but never reaching the brown of *curvispinosus* females. Even old queens were readily distingushed as being much lighter than *curvispinosus* queens.

The length of time that the winged adults were in the nest was quite different in the two species. *L. curvispinosus* began flights soon after the first males and females emerged, and the main flights were over by the time the last males had emerged. In contrast, *duloticus* winged ants stayed in the nest for about a month and seemingly did not begin to fly until after most had become adults.

Males and females reached their height of numbers during the first ten days of August. After that there was a drop in numbers, indicating

flights, but there was no sudden exodus as there had been with *curvispinosus*.

Populations. No total populations could be figured since *duloticus* eggs and larvae could not be distinguished from those of slave species. However total populations in an acorn were recorded for the 10-day periods. These means were: 136.9, 145.2, 156.0, 162.2, 118.3, 120.3, 128.7, 121.3, 115.1. The rather high population in mid-June, rising to a peak in mid-July seems to indicate that these were raiding periods and the sudden drop to 118.3 points to a stopping of raids in late July. This is the time that *duloticus* workers, males and females began to emerge from the pupal stage. By early September eggs and larvae were almost completely gone and the average population of 115.1 was composed of *duloticus* and *curvispinosus* workers plus larvae which were presumably those of *duloticus*. The total mean population in an acorn was 130.9, slightly more than the 100.5 mean population of unparasitized *curvispinosus* colonies.

Worker populations of *L. duloticus* were never large (11.7 per colony). They were lowest in June (5.2 per colony) and rose steadily during August, when pupae were emerging, to a height of 20 per colony in September. The largest number of workers in an acorn was 70, but often there were very few. Of the 270 collections, 167 had 0 to 10 workers, 53 had 11 to 20, 24 had 21 to 30, 13 had 31 to 40, 7 had 41 to 50, 3 had 51 to 60, and 3 had 61 to 70. Worker pupae averaged only 2.7 per colony and were most abundant in mid-July when there were 7.2 per colony.

Wesson reports (1940) that on their raids *duloticus* take not only larvae, but also eggs and pupae. Their captured brood outnumbers their own. Consistently there were more slave workers in an acorn nest than there were *duloticus* workers, the over-all proportion being 4 to 1 (Fig. 3). The greatest proportion of slave workers (7 to 1) came in July and correlated directly with the speed of maturing of brood. Slave pupae also exceeded those of *duloticus* (3.3 to 1). In late June the predominance of slave pupae was enormous (83.4 to 1) because raiding had been vigorous and *duloticus* larvae were just beginning to pupate. Combining the total population of workers plus pupae, we find that for every *duloticus* worker there must have been 3.8 slaves captured.

As would be expected in a parasitic animal, the number of reproductive members was high. During the period when pupae or adults of sexual forms were present in full strength (July 21 to August 20), about 80% of the colonies were producing sexual forms (105 colonies out of 132 collections). These 105 colonies had a mean of 15.5 winged ants, 10.7 being males and 4.8 being females. The average worker population of these colonies was 9.4, giving one worker for every 1.6 winged ants. The 27 colonies not producing winged forms had a mean of 13.0 workers per colony. The greatest number of winged ants in any colony was 88. This consisted of 53 males and 35 females. No colony produced more than 35 females. The highest count of males was 68. Many colonies had only males—47 of the 105. Only 8 had females exclusively and 50 had both.

As collecting progressed, there arose a suspicion that a *duloticus* colony might occupy more than one acorn, perhaps distributing brood over two or three. The mechanics of this would be simple. After a raid some workers might stay in the raided acorn, communication would be maintained with the parent nest, and brood could be carried to the accessory nest to be cared for there.

No direct observations were made of travel back and forth from one acorn to another, but several indirect evidences point to multiple nests.

1. The number of *duloticus* queens was exceedingly low (0.4), yet most colonies without queens did not seem to be dying out, for they had brood and a normal supply of *curvispinosus* workers and brood.

2. During the period when pupae and adults of winged ants were present, a number of acorns had many winged ants but very few *duloticus* workers. It may be that the presence of so many males and females produced a population pressure, perhaps primarily because of their moving about, and some sexual forms, usually males, were segregated into accessory acorns with the usual *curvispinosus* to care for them. Of the acorn collections without queens during the period of sexual forms, 9 had no workers, 20 had one worker each, 18 had 2 workers and 10 had 3 workers. Nevertheless, these exceedingly small groups contained 10.9 winged ants (adult and pupae) per colony. Of these, 9.2 were males and 1.8 were females. This gives 7.5 winged ants for each adult worker in contrast to the figure of 1.6 for populations as a whole. In the 9 acorns with no workers at all, there were 87 adult males, 37 male pupae, 6 female pupae and 2 worker pupae. These, of course, were cared for by *Curvispinosus* workers.

3. The sharp climb of workers per acorn in September seems greater than the emergence of pupae would account for. Perhaps some of this was due to a movement back to a single acorn when flights were over. In correlation with this

the number of colonies with queens was slightly higher than before.

If colonies do spread over several acorns. then the "colonies" listed in this paper might better be called "acorn units."

A slightly different view of the situation may be taken. Wesson (1939) in his study of *Harpagoxenus americanus* Emery, which also enslaves *L. curvispinosus* and *L. longispinosus,* found the presence of "secondary colonies." These were formed when "workers that went to the raided nest did not engage in transporting brood to the home nest but remained and made themselves at home there." Sometimes, during the raid, they carried pupae back from the parent to the captured nest, but subsequently they broke contact with the parent nest. In these secondary nests reproductive functions were assumed by *americanus* workers, which produced not only the expected males but a few females and workers as well. It will be noted that most of the winged ants in the small, queenless *duloticus* colonies were males, but the number seems too great to be produced by the number of workers involved.

Two variations from the usual may be noted. Six times in early summer there were male pupae of *curvispinosus* in a *duloticus* acorn. Evidently these were eliminated before they could emerge, for no adult males were found. No winged females were found, but in two cases dealate queens of slave species occurred. On September 2, a colony contained a *curvispinosus* queen as well as the *duloticus* one, and on September 4 a colony contained a *duloticus* queen plus one of *longispinosus.*

Table II is a summary of comparison of *L. duloticus* with colonies of free-living *L. curvispinosus.*

TABLE II. Comparison of populations of two species of *Leptothorax:* the slave-making *L. duloticus* and the free-living *L. curvispinosus.* Summer of 1955. Edwin S. George Reserve, Livingston County, Michigan

	L. curvispinosus	*L. duloticus*
First worker pupae	already present on June 13	June 28
First male pupae	already present on June 13	June 26
First female pupae	already present on June 13	June 29
First callow workers	June 21	July 21
First adult males	June 23	July 21
First adult females	July 3	July 22
Last worker pupae	still present, Sept. 8	Sept. 5
Last male pupae	July 22	Aug. 10
Last female pupae	July 13	Aug. 10
Last callow workers	still present, Sept. 8	still present, Sept. 8
Last males	Aug. 15	still present, Sept. 8
Last females	July 22	still present, Sept. 4
Time of winged males in nest	41 days	49 + days
Time of winged females in nest	19 days	44 + days
Probable time of main flights	July 7-18	Aug. 15 - Sept. 4
Largest no. of workers in a colony	113	70
Mean no. of workers	28.6	11.7
Mean no. of worker pupae	13.2	2.7
No. of colonies producing sexual forms	51%	80%
Largest no. of winged ants in a colony	62	88
Mean no. of sexuals in colonies producing them	10.9	15.5
Proportion of males to females	1 female to 1.2 males	1 female to 2.8 males
Proportion of workers to sexual forms	2.2 workers to 1 winged	1 worker to 1.6 winged
Mean no. of workers per colony with sexual forms	23.6	9.4
Mean no. of workers per colony without sexuals	15.2	13.0

SUMMARY

1. The rare slave-making ant *Leptothorax duloticus* was found to be fairly abundant in certain parts of oak-hickory woods at the Edwin S. George Reserve, Livingston County, Michigan. In all cases *L. duloticus* enslaved *L..curvispinosus,* and in some colonies a second slave species was found, *L. longispinosus* or *L. ambiguus.* Two hundred and seventy acorn-dwelling colonies were collected for a population study. These showed a mean total population per acorn of 130.9 slaves plus slave-makers. *L. duloticus* averaged 11.7 workers and 2.7 pupae per colony. They produced many males and females. Eighty percent of the colonies had winged ants and these averaged 15.5 a colony. Slave workers exceeded those of *duloticus* 4 to 1.

2. Five hundred and twenty-five collections were made of unenslaved colonies of *L. curvispinosus.* These matured their brood about a month earlier than *duloticus* did and produced fewer males and females. Populations averaged 100.5 per acorn.

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SOME CONTROLLING FACTORS IN THE DISTRIBUTION OF *HAEMATOCOCCUS PLUVIALIS*

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Haematococcus pluvialis, sometimes known as *Sphaerella lacustris,* is a relatively common autotrophic green alga of the order Volvocales. Under favorable conditions it is motile but aplanospores, the dormant stage, are quickly formed in adverse situations. Although it is widely distributed in most parts of the world its occurrence is nearly always limited to small temporary pools. Rocky depressions, concrete basins, birdbaths, and ornamental cemetery urns are typical habitats but it also occurs less frequently in metal containers and road ditches. In a recent study of the rockpool algae on the Tvarminne Archipelago off the southern coast of Finland, Droop (1953) found *Haematococcus pluvialis* to be the most commonly encountered flagellate in temporary pools although it was seldom if ever present in nearby permanent pools and ponds. Many other phycologists have noted that Haematococcus is usually restricted to temporary pools. The factors which allow *Haematococcus pluvialis* to flourish in temporary rocky pools but prevent its growth in permanent bodies of water will be the subject of this communication.

Approximately one half of the material presented in this paper was taken from a thesis submitted to the Graduate School of the University of Missouri in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The research was completed at Yale University where the author was a Fellow in Cancer Research of the American Cancer Society. The author wishes to acknowledge the generous assistance given by Dr. C. L. Kucera of the University of Missouri and Professor G. E. Hutchinson of Yale University.

GROWTH OF HAEMATOCOCCUS IN POND WATER

The most obvious explanation for the distribution of Haematococcus appeared to be either that some favorable factor was present in ephemeral rockpools which was lacking in permanent bodies of water or conversely that some unfavorable factor was present in permanent ponds but absent from temporary pools. In order to test this hypothesis water samples were collected from permanent ponds and used in the preparation of culture medium. If culture medium prepared from pond water would support the growth of Haematococcus it would be reasonable to suppose that the alga could not grow in the ponds because of a suboptimal quantity of light, temperature, or some essential element. If however Haematococcus would not grow in the medium it would be more probable that growth was limited by some toxic substance present in the ponds.

Water samples were collected from 10 permanent farm ponds located in central Missouri. The surface area of the ponds was between 0.1 and 0.3 acre and the average maximum depth was approximately eight feet. Drainage into the ponds was primarily from open pastures and natural grasslands. Livestock was excluded from all the ponds. A rich algal flora was present in the ponds throughout most of the year. Water samples were collected from each of the ponds on four occasions during the spring of 1956. Within two hours following collection each sample was filtered through fine-grade filter paper after which the following salts were added to each liter sample: NH_4NO_3 0.200 gr.; K_2HPO_4 0.200 gr.; $MgSO_4$ 0.200 gr.; chelated iron (Alrose Chemical Company) 0.005 gr.; and soil extract 50 ml. The pH of the medium was adjusted to 7.5 wth N_aOH or HNO_3 when necessary. At this point each sample was divided into two equal parts. Fifty-ml aliquots of one half were placed in 125-ml Erlenmeyer flasks and inoculated with Haematococcus. The other half was autoclaved for two hours at a pressure of 15 lb/in.^{2} pressure. After cooling, 50-ml aliquots of the second half were also inoculated with Haematococcus. As a control Haematococcus was inoculated into medium prepared with distilled water in place of pond water. The three different media, unautoclaved pond water, autoclaved pond water, and the control, were routinely inoculated with enough cells, obtained from a rapidly dividing four- to to seven-day-old culture, to give an initial density of approximately 1000 cells per ml. After inoculation the cultures were allowed to grow for five days, after which the population density of each flask was determined by cell count.

Unfortunately conditions at this time were not very suitable for precise culture work. It was necessary to grow the algal cultures in a green-

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house where, despite protection from direct sunlight and excess heat, there were some flunctuations in the light intensity and temperature. With increasing day length Haematococcus grew faster than it had earlier in the year. For this reason it was necessary, on each sampling date, to compare the growth of Haematococcus in the pond water media with that in the control medium which had been exposed to the same light and temperature fluctuations.

The results of the four months' survey are summarized in Table I. The growth of Haematococcus in the media prepared with unautoclaved and autoclaved pond water is shown as a percentage of that in the control medium.

TABLE I. Relative growth of Haematococcus in medium prepared from unautoclaved and autoclaved pond water collected on four different dates. Growth, as determined by cell count, is expressed as a percentage of that occurring in control medium prepared with distilled water

	Water Unautoclaved				Water Autoclaved			
Date of Collection	2/2	3/18	4/4	5/19	2/2	3/18	4/4	5/19
Ashland Pond No. 1	133	105	33	78	125	108	100	82
Ashland Pond No. 2	121	22	44	106	117	111	115	106
Ashland Pond No. 6	100	81	75	98	75	87	125	86
Ashland Pond No. 7	133	108	33	101	133	108	142	89
Snag Pond	109	105	83	89	96	112	108	82
Rollins Pond	59	100	92	25	69	113	67	82
University Pond No. 1	117	98	87	12	92	74	108	86
University Pond No. 3	121	72	83	98	121	110	100	100
University Pond No. 7	142	23	52	89	142	104	67	94
University Pond No. 8	82	77	67	86	67	91	70	86

The unautoclaved medium prepared from pond water was on many occasions decidedly toxic. Frequently, however, samples collected from the same pond on an earlier or later date were not toxic. Of the 10 ponds sampled only Snag was relatively free of inhibition during the entire four-month period. Samples from all of the ponds except University No. 8 produced, on at least one occasion, growth of Haematococcus comparable to that in the control. In general, autoclaving the water reduced the toxicity to the point where growth was better than in the control.

In addition to the study just described a more intensive investigation was made of the water from Randolph Pond situated about 25 miles from the others. This is a natural sinkhole pond of similar size which receives some drainage from a feedlot and, presumably as a result of this, it supported an even more luxurient algal flora than the other ponds. Water samples were collected approximately every ten days for a period of eight months. The samples were treated in exactly the same manner as those from the other ponds. The results, which are shown in Figure 1, were very similar to those obtained from the earlier survey of the ten ponds.

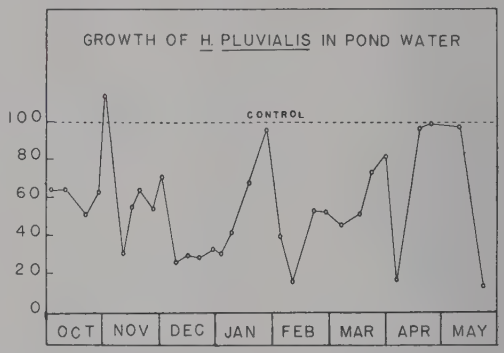

FIG. 1. Growth of *Haematococcus pluvialis* in medium prepared with unautoclaved water collected from Randolph Pond. Growth is shown as a percentage of that occurring in control medium prepared with distilled water.

On several sampling dates water free of inhibiting substances was obtained from Randolph Pond but more often the water was toxic to Haematococcus. The growth of Haematococcus was sometimes improved by autoclaving the water although at other times it had very little beneficial effect. The toxic material could be removed by treating the water with activated carbon. Lefevre *et al.* (1952) and Rice (1954) have reported the presence of heat-labile inhibiting substances in pond water which could be adsorbed upon activated carbon.

Both Lefevre and Rice suggested that the inhibitors were produced by, or at least associated with, algal blooms present in the ponds. This was corroborated by a series of algal counts made in Randolph Pond on the same dates that water samples were taken. During October a heavy mixed bloom of *Anabaena spiroides* and *Microcystis aeruginosa* was present in the pond. Both algae declined during early November until at the end of the first week only a few isolated cells were present. At this time there was no indication of any toxicity in the water although there had been earlier. By November 11 the *Anabaena spiroides* portion of the bloom had returned and the water was again quite toxic. As the Anabaena bloom declined in late November the water became less inhibitory. A bloom of *Cryptomonas* sp. (3000 cells per ml) appeared in the pond in early December and remained until about the middle of January. The water samples collected in December and early January inhibited the growth of Haematococcus. There was a similar

relationship between blooms of Mallomonas in February, *Lyngbya aestuarii* in the latter part of February, and Cryptomonas again in late March. Samples collected from the pond during the latter part of April and early May were not very inhibitory. A great many different algae were present in the pond at that time but no one individual species was particularly abundant.

There was a marked contrast between the lability of the inhibitors present in samples collected during the different blooms. Autoclaving water samples collected at the time of "blue-green" blooms removed all inhibition but it had little effect on samples in which Cryptomonas and Mallomonas were abundant.

From the results of experiments with water from Randolph and other ponds it is apparent that at least one reason that Haematococcus does not occur in permanent ponds is because toxic or inhibiting substances are frequently present. The evidence from the present study as well as that from Lefevre *et al.* (1952) and Rice (1954), suggests that the inhibitors present in natural bodies of water are synthesized by algae. However the evidence is far from conclusive in any of the three cases, Furthermore it is unlikely that the source of the growth-inhibiting substances in natural water can ever be determined until means are available to rule out the activities of microorganisms other than algae. For this reason experiments were undertaken to determine whether an alga grown in bacteria-free medium could produce a substance toxic to Haematococcus.

Algal Competition

Competition in laboratory cultures

Pure cultures of *Chlamydomonas reinhardi* (strain 89) and *Scenedesmus quadricauda* (strain 614) were obtained from the Indiana University Culture Collection through the courtesy of Dr. Richard C. Starr. Strain 34/1a of *Haematococcus pluvialis* was obtained from the Cambridge University Culture Collection. The composition of a medium which was found to be suitable for all three algae is given in Table II. The three algae were grown individually and in various combinations in 125-ml Erlenmeyer flasks containing 50 ml of this medium. The cultures were maintained in a constant temperature light room at 23±1°C and illuminated with "cool white" fluorescent lamps (250-375 foot-candles). Stock cultures of the algae were maintained in test tubes on medium solidified with 2 percent agar. Cultures were examined for bacterial contamination by streaking on peptone and dextrose agar and incubating at 37°C. Experimental cultures were routinely inoculated with 0.5 ml of a rapidly dividing liquid culture. Mixed cultures were inoculated with 0.5 ml of each organism. The population density of cultures was determined five days after inoculation by cell count.

Table II. Composition of medium employed in the culture of *Haematococcus pluvialis, Chlamydomonas reinhardi,* and *Scenedesmus quadricauda*

KNO_3	0.250 g/l
K_2HPO_4	0.100 g/l
$MgSO_4{\cdot}7H_2O$	0.100 g/l
chelated iron*	0.005 g/l
soil extract	50 ml
distilled water	950 ml

*Sequestrene NaFe supplied by Alrose Chemical Company, Providence, Rhode Island.

The results of a typical experiment are shown in Table III. In this instance each of the three algae was grown separately and in the combinations shown. Under these conditions Chlamydomonas invariably either killed Haematococcus or forced it into dormancy within approximately 4-7 days. When Haematococcus and Scenedesmus were grown together there was a mutual inhibition of the two species. If subcultured weekly, however, Scenedesmus soon excluded Haematococcus and began to grow at its normal rate.

Table III. Average number of cells or coenobia (four celled) per ml in one- and two-membered cultures after five days growth

Scenedesmus quadricauda (alone)	149,000 coenobia
Chlamydomonas reinhardi (alone)	3,804,000 cells
Haematococcus pluvialis (alone)	153,000 cells
Scenedesmus quadricauda (together)	57,000 coenobia
Haematococcus pluvialis (together)	45,000 cells
Chlamydomonas reinhardi (together)	3,648,000 cells
Haematococcus pluvialis (together)	All cells dead

This type of experiment was repeated a great many times with pure cultures and with cultures that were deliberately contaminated with bacteria. The results were essentially the same each time, but were modified to some extent by light intensity, pH, nitrogen source, and the available carbon source. For example, under the usual culture conditions Chlamydomonas killed Haematococcus in five days, but when the light intensity was reduced to 30 foot-candles it took 21 days to eliminate Haematococcus completely.

It is easily demonstrated that the inhibition of Haematococcus by Chlamydomonas (or Scenedesmus) is due to an extracellular substance produced by the latter. When Haematococcus is inoculated into cell-free medium obtained by cen-

trifuging a six-day-old culture of Chlamydomonas, death or akinete formation occurs within 24 hours, even though all essential elements are present. The toxicity of Chlamydomonas media is influenced by a number of environmental factors. The inhibitory material has not been identified but the problem is being investigated.

In the course of an investigation concerning competition between different species of algae a number of other incompatible combinations were encountered but to date no alga has been found which is as sensitive to competition as Haematococcus. It is easily inhibited by a large number of algae. A detailed paper dealing with algal compatibilities and modifying environmental factors is planned.

Competition in natural populations

The fact that Haematococcus cannot compete successfully with many common green algae, coupled with the presence of inhibitory substances in ponds, seems to provide the explanation for its absence from permanent bodies of water, but it does little to explain its abundant growth in temporary pools. A possible explanation of this latter point was suggested by some observations of a natural population of Haematococcus.

A very luxuriant growth of Haematococcus was discovered in some shallow metal watering pans in one of the Yale University greenhouses. In this greenhouse it was the customary procedure to water potted plants by placing them in pans which were filled with tap water every 7-10 days. Some water remained in the pans after the soil in the pots was saturated and it was generally five or six days before this excess had completely exaporated. The pans were dry for several days before they were refilled. Motile cells of Haematococcus appeared in these pans about two days after they were filled with water and increased rapidly until evaporation was nearly complete. As the water evaporated the motile cells formed typical brick-red aplanospores. When the pans were refilled motile cells again developed from the aplanospores. This cycle continued in the greenhouse throughout all but the warmest months of the year.

Several preliminary attempts were made to inoculate some of the material from the watering pans into small Pyrex bowls of a more convenient size. These attempts were distinguished only by the regularity with which they failed. Haematococcus grew well in the bowls at first but after the first or second subculture it began to do very poorly, stopped multiplying, and formed aplanospores. Concomitant with the decline of Haematococcus several other algae, usually Chlamydomonas, Scenedesmus, Ankistrodesmus, or Chlorella, became very abundant in the bowls although they were of only minor importance in the pans.

After several such futile attempts it was discovered that unialgal cultures of Haematococcus could be secured and maintained very easily if the inoculum from the pans was dried before it was added to the bowls. In order to study further the role of desiccation in the ecology of Haematococcus twelve bowls of mixed algae were started in the greenhouse. The bowls were left uncovered and no attempt was made to prevent airborne contamination. The medium was the same as that shown in Table II except that it had been diluted to one fifth its concentration with distilled water. The bowls were quite green within one week after inoculation and most of the algae continued to grow in the medium after several subcultures. Some of the more abundant genera that were present in the bowls are shown in Table IV. Some Haematococcus was present in all of the bowls but it was never the dominant organism.

TABLE IV. Algae present in bowls before drying, after drying, and after drying and heating for 24 hours at 70°C

Present in bowls	Survived drying	Survived drying and heating
Chlamydomonas	−	−
Gonium	−	−
Haematococcus	+	+
Hormidium	−	−
Stigeoclonium	−	−
Pediastrum	−	−
Chlorella	+	−
Palmellococcus	+	−
Ankistrodesmus	−	−
Scenedesmus	− & +	−
Navicula	−	−
Nitzschia	−	−
Chroococcus	−	−
Phormidium	−	−

Specific determinations were not made but more than one species of Chlamydomonas, Ankistrodesmus, Scenedesmus, and Navicula were often present in the same culture.

Two weeks after inoculation the cultures had evaporated leaving a layer of dried algae over the walls and bottom of each bowl. With a small piece of damp sterile cotton a little of this dried algal material was swabbed from each bowl, transferred to flasks of sterile medium of the same composition as that used in the bowls, and incubated in a constant temperature (23° C) light room for one week. At the end of this period very few algae were alive. Those which survived drying are indicated in the second column of

Table IV. In contrast to the original cultures, Haematococcus was now the dominant organism in all the flasks, but it did not long remain so in those flasks containing Scenedesmus. After one of two transfers Scenedesmus was the dominant and Haematococcus began to decline.

The ability of different algae to survive desiccation is a very specific trait within even closely related groups. *Scenedesmus quadricauda* is easily killed by drying but *Chlorella vulgaris* cells withstand considerable desiccation. It was noted that one of the species of Scenedesmus in the bowls consistently survived drying while a second species was always killed.

During the summer the rocky pools that form the natural habitat of Haematococcus are frequently exposed to extremely high temperatures. Thus it seemed of interest to determine which algae could survive high temperatures as well as desiccation. Another series of bowls was inoculated with mixed algae and allowed to grow for two weeks. After the medium had evaporated the bowls were placed in a thermostatically controlled oven and held at 70° C for twenty-four hours. After the bowls had cooled, dried material was removed from each and transferred to flasks of sterile medium. The results are shown in the third column of Table IV. Only Haematococcus survived both drying and heating. Dried material removed from the greenhouse pans and treated in the same manner gave similar results. The aplanospores which had been heated required about one day longer to germinate but were otherwise normal. Subsequent tests disclosed that dried aplanospores could withstand temperatures up to 110° C for one hour and still germinate, Otis (1928) noted that dried aplanospores suffered no loss of viability after being stored at room temperature for seven years. Although the aplanospores were quite resistant to dry heat they were readily killed by moist heat at a much lower temperature. Motile vegetative cells were not particularly resistant. They were killed by temperatures of 45° C and were unable to survive desiccation.

Discussion

The widespread occurrence of Haematococcus in temporary rather than permanent bodies of water is due, at least in part, to the fact that such pools are usually free of other competing algae, and not to any inherent characteristic of the pools. Rapid and extreme fluctuations in light, temperature, salt concentration, and even water make conditions extremely severe for almost any form of life. Haematococcus is considerably better suited for survival under these conditions than most algae. Undoubtedly the ability of Haematococcus to withstand adverse conditions depends upon the rapidity with which motile cells can form aplanospores. Resting spores which are capable of withstanding long periods of desiccation and high temperature and yet germinate rapidly under favorable conditions, are readily formed. Droop (1955) has shown that a twenty-four hour period is sufficient for this process. This process may be, and usually is, asexual and can occur at any time in the life cycle. In contrast, the resting stages of many other algae are formed only after several weeks of vegetative growth. The odds against the formation of zygotes by dioecious species in pools that exist for only a few days at a time probably prevent such species from ever becoming very important in ephemeral pools. Furthermore, once formed, the zygotes of many algae are slow to germinate (Starr 1949). For many of the more common algae no specialized resting stages are known. Some are able to withstand desiccation in the vegetative state but many others are unable to do so.

Haematococcus, like many other Volvocales, requires a relatively rich medium for growth. The nitrogen content of most oligotrophic lakes is far too low ever to support any detectable growth of Haematococcus. The salt content of small highly eutrophic ponds would be more suitable but it is also suitable for a large number of other rapidly growing algae which are able to produce a substance, or substances, which are inhibitory to Haematococcus. In the present study competition experiments were restricted to the green algae but in view of the published reports by Flint and Moreland (1946), Von Denffer (1948), Reich and Aschner (1947), Harder and Oppermann (1953) and Jakob (1954) that antibiotic substances are produced by algae belonging to most of the major divisions it would be quite surprising if Haematococcus were inhibited only by members of the Chlorophyceae.

At the present time it is impossible to say with any assurance whether all or even part of the inhibitory material present in farm ponds is algae-synthesized. It might be the result of bacterial or fungal action. Data from Lefevre (1952), and Rice (1954), as well as from the present study, suggest that the algae are responsible but until something definite is known regarding the chemical nature of these inhibitors it would seem best to leave it as an open question. In the case of the greenhouse watering pans

there is little doubt that at least several of the algae were producing material inhibitory to Haematococcus. Fortunately for Haematococcus these species could not survive desiccation and consequently all competition was eliminated once each week. When the pans were filled with water and never allowed to become completely dry the other species increased and vegetative cells of Haematococcus disappeared. When the pans were allowed to dry, Haematococcus was again abundant.

Not all algae are toxic to Haematococcus. The results of an experiment very similar to the present one were reported by McVeigh and Brown (1954). They compared the growth of *Haematococcus pluvialis* and *Chlamydomonas chlamydogama* in individual and mixed cultures, and found only weak mutual inhibition or slight inhibition of Chlamydomonas by Haematococcus. They employed slightly different culture methods but some of their studies were repeated by this investigator using higher light intensities and a slightly different medium without obtaining any results to suggest that *C. chlamydogama* could inhibit *H. pluvialis*. *C. chlamydogama* is not a very desirable species to use in competition studies, however, as it is an auxotrophic species and never grows very well in liquid medium even when alone.

During the study of the eleven farm ponds in Missouri it was noted that samples from Snag Pond showed less inhibition than any of the others. Snag Pond, which in many respects is more bog-like than pond, contained large quantities of rooted aquatic plants as well as a number of different algae, particularly desmids. The water was usually slightly acid. During the summer of 1955 several acid bog lakes in northern Michigan near the University of Michigan Biological Station were assayed for substances toxic to Haematococcus. These lakes were also consistently free of inhibiting material. One might therefore expect Haematococcus to occur in these lakes were it not for the fact that, as pointed out much earlier by Pringsheim (1914), Haematococcus is quite sensitive to acid and grows best in neutral or basic medium.

Summary

Haematococcus pluvialis, a motile green alga, is a common occupant of ephemeral rainwater pools but does not occur in permanent ponds. An explanation is offered for this limited distribution based upon the observations that:

1. A substance, or substances, is frequently present which inhibits the growth of Haematococcus even though all essential growth elements are present. This inhibiting substance is associated with algal blooms in the ponds.

2. Pure cultures of *Chlamydomonas reinhardi*, and to a lesser extent *Scenedesmus quadricauda*, produce an extracellular substance which is toxic to Haematococcus.

3. Few algae, other than Haematococcus, are capable of surviving the extremely severe environmental conditions that prevail in ephemeral rockpools. Haematococcus possesses a number of morphological features which allow it to grow and survive in these pools where it is relatively free from competition by other algae.

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FURTHER RESULTS IN THE STATISTICAL ANALYSIS OF STREAM SAMPLING

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INTRODUCTION

Recently, Gaufin, *et al.* (1956) have analyzed the sampling of stream bottoms for macro-invertebrate fauna. A method was presented for computing the average number of species detected in k' samples, say $S_{k'}$, based on the number and distribution of species observed in n samples, where $n \geqq k' \geqq 1$. This method involves calculating the average number of *new* species, s_k, contributed by the k-th successive sample, $1 \leqq k \leqq k'$, according to the formula

$$s_k = \sum_{i=1}^{n-k+1} a_{i,k} s_i \qquad (1)$$

where s_i denotes the number of species observed in i of the n samples and the $a_{i,k}$ are certain coefficients defined in the published paper. Then, $S_{k'}$ is obtained by summing:

$$S_{k'} = \sum_{k=1}^{k'} s_k \qquad (2)$$

The present paper offers a formula for estimating the standard deviation of the number of species detected after k' samples. This formula makes use of results obtained by applying equations (1) and (2). An estimate of variability, taken together with an estimate of mean, provides additional basis on which to judge the adequacy of sampling and may serve to guide future sampling plans.

DERIVATION OF PROPOSED FORMULA

Suppose that before any sampling is undertaken, a population of N undetected species resides in the area. As more and more samples are drawn, and previously undetected species observed, this population diminishes. We estimate that on the average, after the k'-th sample has been drawn, the number of undetected species has diminished to $N - S_{k'}$.

Now, if we imagine a continuous sampling process, rather than a withdrawal of discrete samples—in other words, if k is thought of as a continuous variable, like time (not unreasonable, in view of the time-consuming search required to discover and identify all the species present in a sample)—then the decline in the number of undetected species becomes amenable to a theoretical treatment discussed by Kendall (1948). Specifically, if $\mu(k)$ denotes the rate of decline in the number of undetected species—this rate changing as sampling continues and therefore, a function of k—then the average number of undetected species at a given point k' in the sampling process is

$$(N - S_{k'}) = N_e^{-\rho'}, \qquad (3)$$

where $\rho' = \int_0^{k'} \mu(k)\, dk$, and $e = 2.718\ldots$ is the base of the natural logarithms. Further, the variance of the number of undetected species at k' say $V_{k'}$, equivalent to the variance in the number of observed species at k', is

$$V_{k'} = N_e^{-2\rho'} \int_0^{k'} e^{\rho'} \mu(k)\, dk \qquad (4)$$

The square root of this variance (*i.e.*, the standard deviation) is the desired quantity. Equations (3) and (4) are among many derived by Kendall (1948) in connection with probability processes involving numbers of individuals whose rates of increase or decrease are generally functions of time.

The function $\mu(k)$ is unknown to begin with, but may be revealed by determining a relationship between $S_{k'}$, which is known from equations (1) and (2), and k'. The data used for this purpose were introduced in the 1956 paper. They arose from a special series of samples taken in a small midwestern stream, Lytle Creek, which has been the subject of extensive research by the Public Health Service (United States Department of Health, Education, and Welfare) (Gaufin and Tarzwell 1952). Two sections of the creek were sampled and a total of sixty samples collected; ten each from a marginal, pool, and riffle area at each station. These areas are designated respectively, by station, as 1a, b, c, and 2a, b, c.

TABLE I. Average number of species ($S_{k'}$) observed in sets of k' samples, by station

	STATION					
k'	1a	1b	1c	2a	2b	2c
1	17.8	14.9	21.1	22.3	15.7	25.3
2	25.3	21.5	28.1	32.2	24.0	33.3
3	30.6	26.8	32.5	39.0	30.1	38.1
4	34.8	31.2	35.6	44.2	35.0	41.8
5	38.3	35.2	37.9	48.4	39.2	45.0
6	41.2	38.6	39.8	52.0	42.6	47.7
7	43.8	41.8	41.3	55.2	45.5	50.2
8	46.0	44.7	42.7	58.0	48.0	52.4
9	48.0	47.4	43.9	60.6	50.1	54.3
10	50	50	45	63	52	56

Table I presents the successive values of S_k' observed at each station. The following general equation appears to describe closely the results at all sampling areas:

$$S_k' = a + bk'^q, \ (1 \leq k' \leq 10) \qquad (5)$$

where the values of a, b, and q may vary from station to station. The term a is necessary, in general, to account for a relatively large value of S_1, the average number of species detected in single samples. The extent to which equation (5) holds for $0 \leq k' < 1$ is of no practical importance since we are interested only in standard deviations for $k' \geq 1$, and, as shown below, define the final variance equation so that, for $k' = 1$, it reduces to the observed value, V_1.

Of the three constants in this equation, the exponent q was estimated first. According to equation (5),

$$D_k' = S_{k'+1} - S_k' = bk'^q \left[(1 + 1/k')^q - 1\right]$$

Expanding the right-hand side in binomial series,

$$D_k' = b \left[qk'^{q-1} + \frac{q(q-1)}{2} k'^{q-2} + \ldots . \right].$$

Since q will be small, usually less than ½, D_k', is approximately equal to bqk'^{q-1}, at least for $k' > 1$. Therefore, plotting successive differences D_k' against $k' > 1$ on log-log paper will yield an approximately linear relation, whose slope is an estimate of $q - 1$. Two such graphs are given in Figure 1. Straight lines were fitted by eye and slope was determined as

$$\frac{\text{Log } (D_2) - \text{Log } (D_{10})}{\text{Log } 2 - \text{Log } 10}$$

where the points in the numerator were taken from the fitted line. Adding unity to each slope provided the estimate of q at that station. Then, S_k' was plotted against k'^q and the constants a and b estimated by the usual least squares formulas for fitting a straight line. All these calculations are set forth in Table II, using station 2a as an example. Table III lists q and b at each station.

Figures 2-5 show good agreement between the observed S_k' and the fitted model, equation (5). To conserve space, $q = .30$ was used at stations 1a, 2a, and 2c and results at these stations plotted on a single graph.

Returning to equations (3) and (4),

$$N - S_k' = N_e^{-\rho'} = N - (a + b\,k'^q),$$

whence $\rho' = \int_0^{k'} \mu\,(k)\,dk = -\text{Log}_e\,(A - Bk'^q),$

(6)

in which $A = 1 - a/N, B = b/N.$

Then, $\mu' = \dfrac{d\rho'}{dk'} = \dfrac{Bqk'^{q-1}}{A - Bk'^q},$ (7)

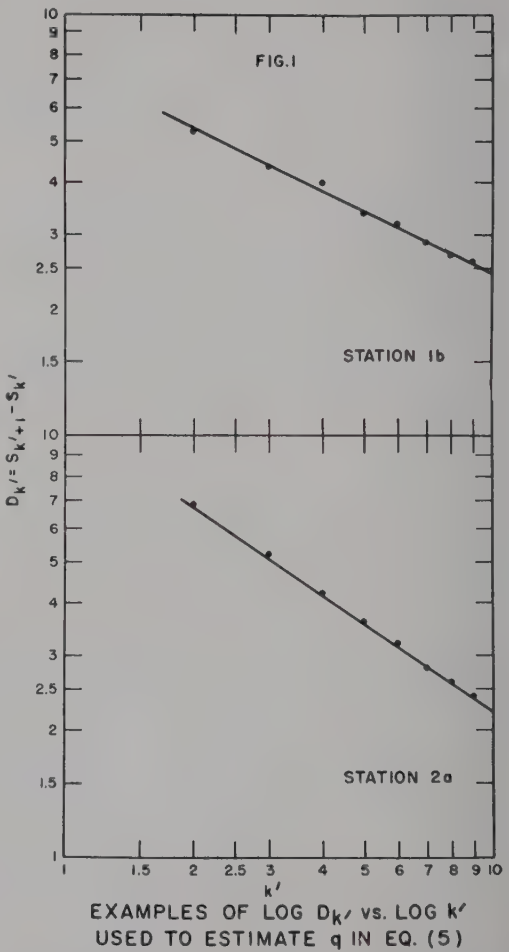
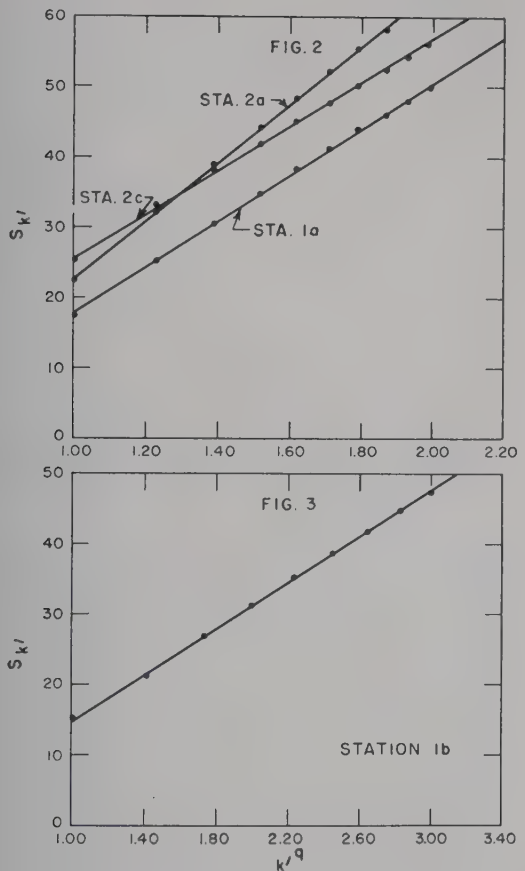
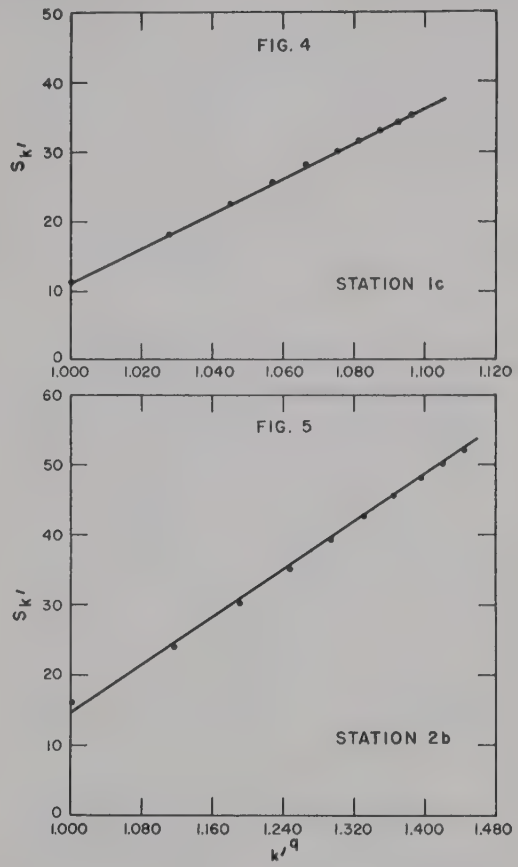


FIG. 1. Examples of log D_k' vs. log k' used to estimate q in eq. (5).

where μ' is the rate of decline in the number of undetected species at the point of drawing the k'-th sample. In these equations μ is a relative rate, exactly equivalent to an instantaneous life-table death rate—*i.e.*, deaths (corresponding here to new species detected) occurring in a small interval of time dt (or sampling dk) divided by the number of individuals (here undetected species) surviving to the beginning of the interval. Equation (7) may seem rather complicated, but is, in fact, a generalization of a so-called "retardant" formula used frequently in water pollution studies to describe the oxidation rates of certain waste products (Phelps 1947, p. 120-121). The rate of action is not constant, but decreases as the process



MEAN NUMBER OF SPECIES OBSERVED AFTER k′ SAMPLES ($S_{k'}$) vs. k'^q, BY STATION



FIGS. 2-5. Mean number of species observed after k' samples ($S_{k'}$) vs. k'^q, by station.

continues—essentially a law of diminishing returns.

Substituting equations (6) and (7) into the variance equation (4),

$$V_{k'} = N(A - B_{k'^q})^2 \int_o^{k'} \frac{B\,q\,k^{q-1}}{(A - Bk^q)^2} dk$$

$$= b\,k'^q\,(1 - B/Ak'^q) \qquad (8)$$

One difficulty remains since the ratio B/A is unknown. To overcome this, we resort to V_1 which may be estimated directly as the variance of the number of species found in single samples. In accordance with equation (8), set this estimate equal to $b(1 - B/A)$ and estimate

$$B/A = 1 - \frac{V_1}{b}.$$

Inserting this value of B/A into (8), compute variances and standard deviations for $k' > 1$. These estimates are, then, partly dependent upon the variance observed among the indidividual samples. Additional reason exists, therefore, for drawing a large number of samples during initial survey and carefully selecting the samples to achieve, as far as possible, representation from all the habitats in the area.

It is always possible, of course, to estimate the total population N—by simple graphic extrapolation of $S_{k'}$, for example—and use this estimate rather than V_1 to evaluate B/A. However, such procedure would ignore the fact that areas containing the same populations may differ widely in the variability among samples because of differences between areas in numbers of individuals per species and in the uniformity with which these individuals are distributed over the bottom. We are, therefore, on much safer ground if we relate variance estimates to V_1 even though this observed value may be subject to considerable random sampling error.

It may be noted that $V_{k'}$ as given by equation

TABLE II. Example of calculations involved in estimating standard deviations, based on eqs. (5) and (8): Station 2a

k'	$S_{k'}$	$D_{k'} = S_{k'+1} - S_{k'}$ $(k' > 1)$	(k'^q)*	$(V_{k'})$§,†	Std. Dev. $= \sqrt{V_{k'}}$
1	22.3	...	1.00	28.71 (Observed)	5.4
2	32.2	6.8	1.23	31.72	5.6
3	39.0	5.2	1.39	33.12	5.8
4	44.2	4.2	1.52	33.80	5.8
5	48.4	3.6	1.62	34.04	5.8
6	52.0	3.2	1.71	.....	
7	55.2	2.8	1.79	. .	
8	58.0	2.6	1.87	. .	
9	60.6	2.4	1.93	.....	
10	63.0	...	1.99		

*Estimated $(q-1)$ = Slope of line fitted by eye to Log $D_{k'}$ vs. Log k' $(k' > 1)$ (see Fig. 1*b*) = $\frac{\text{Log } D_2 - \text{Log } D_{10}}{\text{Log } 2 - \text{Log } 10}$, taken from line, = $\frac{\text{Log } 6.80 - \text{Log } 2.21}{.6990}$ = − .70. Hence, estimated $q = -.70 + 1 = .30$

§Estimate linear constants a and b from least-squares fit of $S_{k'}$ vs. k'^q:

Est. $b = \frac{\Sigma S_{k'} k'^{.3} - 1/10\ (\Sigma S_{k'})\ (\Sigma k'^{.3})}{\Sigma (k'^{.3})^2 - 1/10\ (\Sigma k'^{.3})^2} = \frac{800.22 - 762.21}{26.690 - 25.760} = 40.87$

Est. $a = 1/10\ (\Sigma S_{k'} - b\ \Sigma k'^{.3}) = 1/10\ (474.90 - 655.96) = -18.11.$

†Variance estimate, $V_{k'} = bk'^q\ (1 - B/A\ k'^q)$, where $B/A = 1 - \frac{V_1}{b}$. At Station 2a, $V_1 = 28.71$. Therefore, $B/A = 1 - .70 = .30$. Then, $V_2 = b2^q\ (1 - B/A\ 2^q) = 40.87 \times 1.23\ (1 - .30 \times 1.23) = 31.72$; $V_3 = 40.87 \times 1.39\ (1 - .30 \times 1.39) = 33.12$, etc.

TABLE III. Estimated values of q and b in eq. (5), by station

	Station					
	1a	1b	1c	2a	2b	2c
q.....	.31	.50	.04	.30	.16	.29
b.....	32.54	16.30	49.01	40.87	83.47	30.68

(8) will attain a maximum for that integral value of k' which comes closest to solving the equation,

$$k'^q = \frac{A}{2B} = \tfrac{1}{2}\ \frac{b}{(b - V_1)}.$$

When $V_1 \leq \tfrac{1}{2}b$, $V_{k'}$ is greatest at $k' = 1$ and declines thereafter.

Occasionally, by chance variation in V_1, the estimated value of B/A may turn out negative (this occurred at station 1b), leading to a continually increasing $V_{k'}$. In fact, of course, the variance must eventually decline to zero since any sufficiently large number of samples would reveal the entire population of species. In such cases, the proposed method should not be trusted beyond, say, $k' = n/2$. In view of the dependence of the method on the observed V_1 this may be a wise rule to follow generally.

Only wider experiance can determine the general applicability of equation (5) to other sampling results under a variety of conditions. Kendall's equations (3) and (4) provide a framework on which to impose any relation between $S_{k'}$ and k' that seems to fit a particular set of data. Thus, if S_k is given by some function $f(k)$, then

$$V_{k'} = [f(k') - f(0)]\ [1 - \frac{f(k') - f(0)}{N - f(0)}].$$

The constant $C = \frac{1}{N - f(0)}$ may be estimated from the observed variance V_1 according to the general formula,

$$C = \frac{f(1) - f(0) - V_1}{[f(1) - f(0)]^2}$$

Empirical Method of Estimating Standard Deviations

There is a laborious but independent method of estimating the desired standard deviations, whose results may be compared with those given by equation (8). Suppose the ten samples collected at each station were separated into five pairs, *e.g.*, sample numbers (1, 2); (3, 4); (5, 6); (7, 8); (9, 10). The number of different species in each pair of samples may be counted and the variance of these numbers calculated. Other groups of pairs may be obtained by interchanging the members of each pair. In all, 945 such groups may be derived from the original ten samples. Each of these groups contributes an estimate of the variance of the number of species detected by independent pairs of samples. Of course, these estimates are highly correlated; nevertheless, their mean is an unbiased estimate of V_2. Similarly, groups of triplets, quadruplets, and quintuplets may be prepared, each k-tuple composed of k samples which are not represented in any other k-tuple in the same group. The average variance of the number of species detected by the sets of samples in a group is an estimate of $V_{k'}$.

A punched card was prepared for every species found at a given sampling site, indicating by a 1- or 2-punch, respectively, the presence or absence of that species in each of the ten samples at the site. The number of different species in each set of k samples was determined by a sequential sorting procedure. Average variances and their square roots—the standard deviation—were computed for $k' = 2$ and 5. Table IV compares these standard deviations with those computed from equation (8). Standard deviations obtained from this equation for intermediate values of k' are also included.

Discussion

In general, the two methods show good agreement. However, the differences at Station 2c, namely, an increasing standard deviation by the

TABLE IV. Standard deviation of the number of species detected after k' samples ($k' \leq n/2$), by station, calculated according to two methods; $n = 10$ samples

Station	k'	Method		Station	k'	Method	
		Empirical	Formula (Eq. 8)			Empirical	Formula
1a	1*	...	5.7 species	2a	1	...	5.4
	2	6.2	...		2	5.7	...	5.6
	3	...	...		3	...	...	5.8
	4	...	...		4	...	...	5.8
	5	6.6	...		5	5.3	...	5.8
1b	1	...	4.5	2b	1	...	7.1
	2	5.1	...		2	6.9	...	7.1
	3	...	...		3	...	...	7.3
	4	...	...		4	...	...	7.3
	5	6.6	...		5	5.9	...	7.3
1c	1	...	4.8	2c	1	...	3.8
	2	4.4	...		2	4.0	...	3.6
	3	...	...		3	...	...	3.3
	4	...	...		4	...	...	2.9
	5	3.7	...		5	4.8	...	2.5

*Estimated directly from numbers of species found in individual samples.

empirical method of estimation, but a declining one by the theoretical method, indicate that they do not measure exactly the same thing. The empirical method is especially sensitive to lack of uniformity in the distribution of species found in only one sample. Thus, if several such species happened to reside close together, they would swell the yield of one or two fortunately chosen samples, but be unavailable to samples taken elsewhere. For example, of 17 species found only in single samples at Station 2c, 12 (71%) occurred in samples 2, 4, or 8. In such a case, a set of three samples, say, consisting of two especially fruitful samples and one average sample offers a total yield considerably greater than a set of three average samples. This situation leads to an increasing standard deviation under the empirical method of estimation.

The theoretical method reflects nonuniformity in the distribution of such uncommon species only through its partial dependence upon the observed variance in the individual samples, V_1. The latter may be a rather insensitive index of such nonuniformity. At Station 2c, V_1 was unusually small—about half the mean number, S_1, despite the fact that certain samples had an unusually large share of the one-sample species. As brought out in its derivation, the proposed theoretical formula depends largely on the rate at which new species are detected by successive samples, especially early samples. This rate is based not on the uniformity with which uncommon species are distributed among the samples, but rather on the proportions of the total number of species represented by uncommon, intermediate, and common types, respectively.

Therefore, the writer feels that the proposed formula reflects a more general picture of species distribution than the empirical method with which it has been compared. In any case, the latter method is too cumbersome for routine use.

APPLICATION

Standard deviations will shed light on the efficiency of present sampling and may thereby serve to guide future sampling. In particular, if routine surveys are planned, we must know the minimum number of samples required to provide an adequate list of the species present in an area. As a mechanism for checking the pollutional status of a stream, such a list need not approach completeness, since the relative change in the number of species over time and the nature of the species found (*i.e.*, pollution-tolerant or pollution-sensitive) are more important than the actual number at any given time. Results at three of the areas studied here illustrate the way in which this minimum number of samples may be ascertained.

At Station 2b, the estimate $\sqrt{V_1}$ was unusually large, due chiefly to one completely barren sample. However, the standard deviation did not increase materially with increasing numbers of samples, indicating that despite one poor choice, sampling was fairly efficient in uncovering species of diverse distributions in this area. From Table I we note that the rate of detection, slow at first, picked up rapidly. After three samples 58 percent of the species found in ten samples had already been observed, on the average. Review of the species list (also see Table I in Gaufin *et al.*, 1956) showed that the percentage of species found in single samples was not excessive (36.5 percent compared to an average of 36.7 percent over all stations), nor was the percentage found in all

fruitful samples particularly low (11.5 percent compared with an average of 11.7 percent).

We may conclude that a minimum of four samples selected with care to eliminate the possibility of a sterile sample, should yield an adequate faunal picture at Station 2b. To check this conclusion, standard deviations were computed for the nine fruitful samples, resulting in a 30 percent reduction in $\sqrt{V_1}$ and a steadily declining standard deviation thereafter. By the fourth sample, the estimated standard deviation was only ± 11 percent of the mean number of species detected.

Prospects at a station like 1b are not nearly so optimistic. By contrast with 2b, variation among individual samples was not great, yet $\sqrt{V_{k'}}$ increased sharply with k' New species must have been detected at a slow rate, despite the fact that sampling was performed with care. Table I confirms this: at Station 1b, 54 percent of species found after ten samples were observed, on the average, after three samples, whereas over all stations an average of 63 per cent were observed after three samples. By reviewing the species list, this relatively low rate of detection was traced to a high percentage of single-sample species (52 percent of all species detected, compared with 37 percent at the average station), almost all represented by only one individual apiece. The only solution here is to examine as many carefully selected samples as time and labor will allow.

Station 1c represents an extreme as does Station 1b, but in this case, one of steadily declining variability. Since $\sqrt{V_1}$ was only average (in fact, slightly greater than at 1b), the basis for the changing standard deviation must, again, be the rate of detection—unusually rapid at Station 1c. Table I shows that three samples uncovered, on the average, 72 percent of species observed in ten samples at this station. This rapid rate of detection was based on a relatively low percentage of species (24 percent) found in only single samples and a relatively high percentage (18 percent) found in all ten samples. Station 1c represents an area where invertebrate species are rather well distributed over the stream bottom. Under these conditions, a minimum of two samples, selected with reasonable care, should suffice in routine surveys.

Summary

1. A formula (equation 8) is proposed for computing the variance (or standard deviation) of the number of species observed in independent sets of k' samples, based on data supplied by a study series of $n > k'$ samples. An example of the necessary calculations is included.

2. This formula is applied to observations of macro-invertebrate bottom fauna in six areas of a midwestern stream. The same data have been used earlier (Gaufin *et al.* 1956) to illustrate a procedure for estimating the mean number of species in k' samples.

3. Results using the proposed formula are compared with those given by a laborious empirical method which involves counting the number of species found in many different sets of k' samples. Agreement between the two methods is generally good, but the former seems to reflect a more general picture of species distribution in the area.

4. Use of these results to determine the number of samples for future surveys is discussed. The importance of drawing a large number of carefully selected study samples is emphasized.

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THE PLEISTOCENE HISTORY OF TEMPERATE BIOTAS IN MEXICO AND EASTERN UNITED STATES

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Introduction

The fate of the warm temperate biota of eastern United States during a glacial maximum is one of the intriguing problems in Pleistocene biogeography. Various authorities (see especially Deevey 1949: 1374-5) view the time of ice advance as one in which cool periglacial climates extended far beyond the ice border, driving warm temperate animals and plants into two major refugia, peninsular Florida and Mexico. Relicts

of such a southward withdrawal would not be likely in Florida today because of the lack of topographic diversity to provide habitats for temperate species after postglacial climatic amelioration. However, the mountains of Mexico should, at least in theory, offer refuge to animals and plants reaching this latitude from the north in the Pleistocene.

An opposing view is taken by Braun (1955: 315) who contends that temperate plants reached Mexico from the United States at the latest by the middle Cenozoic, that they were isolated there by arid Pliocene environments, and that pluvial periods in the Pleistocene provided opportunities only for xero-mesophytes to cross this barrier. Our purpose is to consider the distribution of terrestrial vertebrates in relation to the problem and to compare these data with the floristic information.

In the following analysis we shall speak of dispersal between eastern United States and Mexico. The implied direction of north to south is a convenience and does not exclude dispersal in the opposite direction, as favored by McVaugh (1952: 321). In addition to the plant phylads he lists, there are morphological grounds for believing that *Diadophis* (Blanchard 1942: 131-132), *Reithrodontomys* (Hooper 1952: 206), *Thamnophis* (Ruthven 1908: 187-194) and various other animal phylads have spread into eastern United States from the Mexican Plateau.

Evidence from a variety of sources suggests that considerable Pleistocene climatic change was felt at low latitudes (Emiliani 1955; Hora 1953; Sears and Clisby 1955; Zeuner 1951). In the interpretation of biotic relationships we will have to consider the nature of the postulated climatic changes and their relationship to high-latitude events.

The biogeographic evidence of Pleistocene dispersal and climatic change in Middle America appears represented in the following: (1) disjunct distributions in the ranges of certain mammals (Burt 1949), birds (Griscom 1950: 371-3), reptiles and amphibians (Martin 1955b), and plants (Braun 1955: 315); (2) mid-continent hybridization zones in closely related species of *Quiscalus* (grackles), *Colaptes* (flickers), *Sturnella* (meadowlarks), and *Icterus* (orioles) following renewed contact of populations isolated in southeastern and southwestern refugia; (3) rather meager but impressive fossil mammal records from the late Pleistocene of northeastern Mexico, including species unknown this far south at present, i.e. *Marmota, Cervus, Erithizon* and *Synaptomys cooperi* (Cushing 1945; Gilmore 1947); (4) pollen profiles indicating *Picea* (spruce) in the Austin region of south Texas (Potzger and Tharp 1947, 1954) and in the Valley of Mexico (Sears and Clisby 1955).

From this the question arises, how much of the distributional relationship between North and Middle America can be attributed to Pleistocene climatic change?

Pleistocene Relicts or Tertiary Relicts?

We are concerned with the biotic history of the humid montane forests found along the escarpments of the Mexican and Guatemalan Plateaus. Close relatives of the modern flora of these escarpments appear in early Cenozoic deposits. Thus MacGinitie (1941: 122) finds abundant *Liquidambar* leaves in Eocene clays from the Central Sierra Nevada. Certain of these have their modern counterparts in the three-lobed leaf form of modern Mexican populations of *L. styraciflua* and in the Chinese *L. formosana.* "The presence of abundant 3-lobed leaf forms directly relates the fossil species to the living variety in Mexico." A close correspondence between the modern Mexican escarpment flora and the Eocene Wilcox is noted by Sharp (1951).

In view of this fossil record it is not surprising to find close relatives of many common Cloud Forest trees in other Tertiary refuges such as eastern United States and eastern Asia. Vicariads of the Cloud Forest flora in the United States occur almost entirely within the Deciduous Forest Formation (Fig. 14) of Braun (1950). In Mexico they are confined largely to isolated patches of humid montane forest, typically in the Sierra Madre Oriental. Occasionally certain species such as white pine and sweet gum appear at low elevations in wet tropical forest; however, most are confined to the mountains above 1000 meters. Such eastern "temperate" genera as *Liquidambar, Fagus, Nyssa, Carpinus, Acer* (hard maple group), *Mitchella,* and *Hamamelis* occur in Mexican Cloud Forest with *Meliosma, Podocarpus,* and *Eugenia,* a striking mixture of northern and southern hemisphere genera.

Miranda and Sharp (1950) describe various areas in eastern Mexico and Guatemala where such forests occur. Figures 1-8 illustrate the range of certain species in the "eastern temperate element". Dressler (1954) illustrates others. Among the mosses Crum (1951) lists 125 species with a similar disjunct distribution. *Pinus strobus* (Fig. 1) has the most extensive gap in its range; however, none of the species in question occurs between eastern Texas and the mountains of northeastern Mexico, a gap of at least 500 kilometers. *Liquidambar styraciflua* (sweet gum, Fig. 2) is probably the most

abundant member of the "eastern temperate element" in the montane forests. *Carpinus caroliniana* (blue beech, Fig. 3) is slightly less common in the Sierra Madre Oriental but reaches the Sierra Madre Occidental. Among the rarer relicts are *Fagus* and its root parasite, *Epifagus* (in Fig. 4 the range of the former is shaded and that of the latter is indicated by dots). Hard maple (*Acer skutchii* in Middle America) is also poorly known in comparison to sweet gum, although it reaches Guatemala (Fig. 5). *Nyssa sylvatica* (sour gum, Fig. 6) has an abbreviated Mexican range. Closely related species in *Taxus* (yew, Fig. 7) and *Illicium* (Fig. 8) have rather restricted distributions east of the Mississippi.

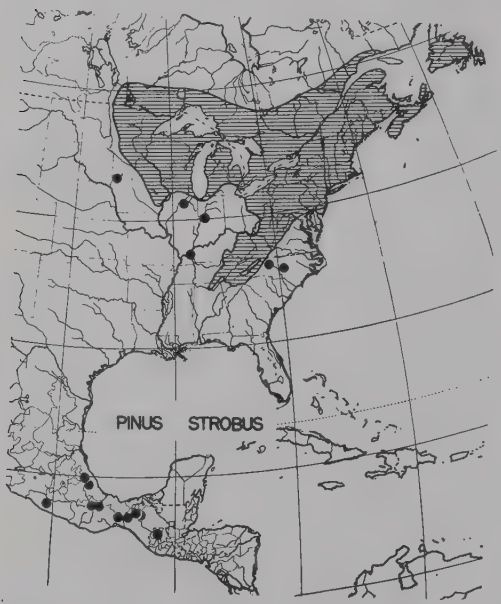

FIG. 1.

Although the species or species pairs whose ranges we illustrate are of reasonably close relationship, no reliable modern revisionary studies have been undertaken to determine the precise degree of taxonomic affinity between Mexican and United States populations. It is possible, for example, that *Illicium floridanum* and *I. mexicanum* represent the same species. Conversely Mexican populations of *Liquidambar* may prove distinct from those of eastern United States. In the absence of such revisions a comparison of possible evolutionary rates between related species in Asia, Middle America, and eastern United States is premature.

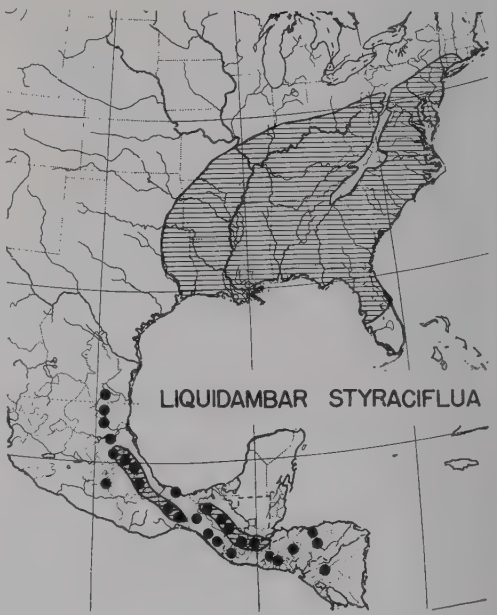

FIG. 2.

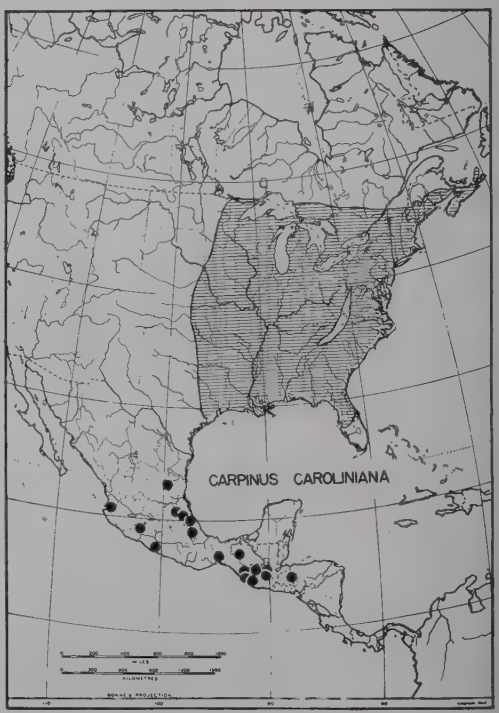

FIG. 3.

FIG. 4.

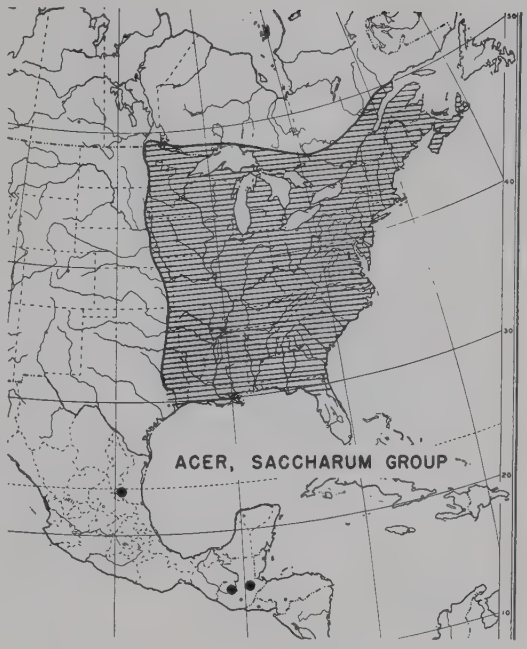

FIG. 5.

Dressler, Sharp (1953), and Crum have assigned a late Pliocene-Pleistocene time to the arrival of the eastern temperate element in Mexico. If accidental transport via winds, birds, etc., is not involved, a mechanism they do not propose, their hypothesis requires the development of a Pleistocene forest corridor, or at least a transitory spread of temperate forest, across the plains and isolated mountains of northern Mexico and south Texas. Today this region is covered with arid grassland and thorn scrub. To produce conditions suitable for a corridor of mixed mesophytic forest with beech, white pine, sugar maple, sour gum, sweet gum, evergreen magnolia, etc. would require both cooler and much wetter climatic conditions.

An alternative to the Pleistocene hypothesis has been advanced by Dobzhansky and Epling (1944), McVaugh (1952), Steyermark (1950), and especially Braun (1955). Braun concedes that certain xero-mesophytes such as *Juniperus* and *Cercis* probably re-established contact across the Texan hiatus during the Pleistocene. Nevertheless the more mesophytic members of the flora such as *Fagus, Acer skutchii,* and *Mitchella* she views as remnants of a much older separation. This temperate element represents a major part of the Arcto-Tertiary flora which reached the highlands of Middle America in mid-Cenozoic at the latest. Subsequent development of a semi-desert or steppe barrier in northern Mexico from the Pliocene through the Pleistocene effectively isolated the humid montane flora. Paleobotanical support of Braun's interpretation stems less from a doubtful record of Miocene *Liquidambar* on the Isthmus of Tehuantepec (Berry 1923) than from the great importance of the Mexican escarpment as a refugium for living members of the Eocene Wilcox Flora (Sharp 1951).

A rough test of these two phytogeographic views can be made by examining the fauna of the montane Mexican forests. If a forest corridor of Pleistocene age brought temperate eastern United States trees and other plants into (or out of) Mexico, we may expect unmistakable faunal evidence of this event. However, if the forest connection is more ancient, as Braun asserts, any residual faunal evidence should accordingly be less obvious and at a higher taxonomic level.

Relicts at Rancho del Cielo

In studies on terrestrial vertebrates in humid montane forests of eastern Mexico our field work has centered on an isolated outpost of Cloud Forest at Rancho del Cielo in southwestern Tamaulipas (Harrell 1951; Hernández *et al.* 1951;

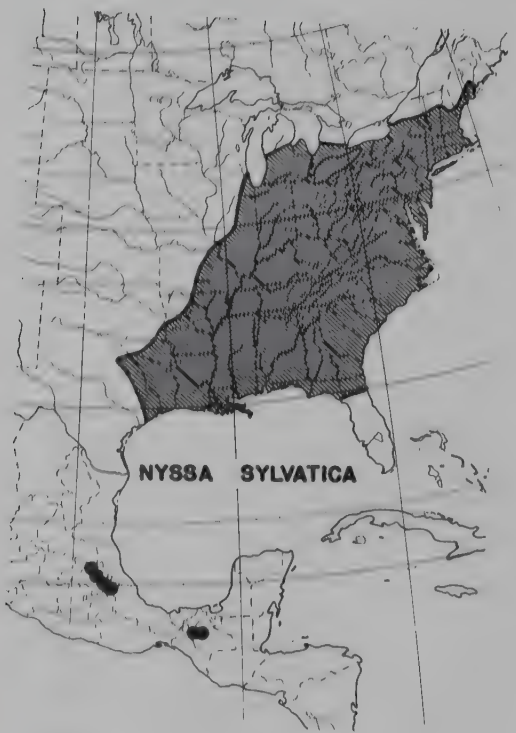

Fig. 6.

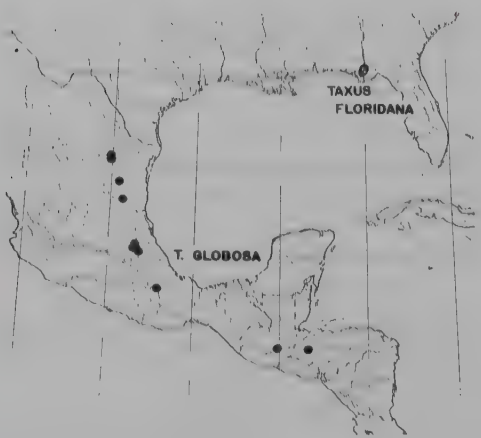

Fig. 7.

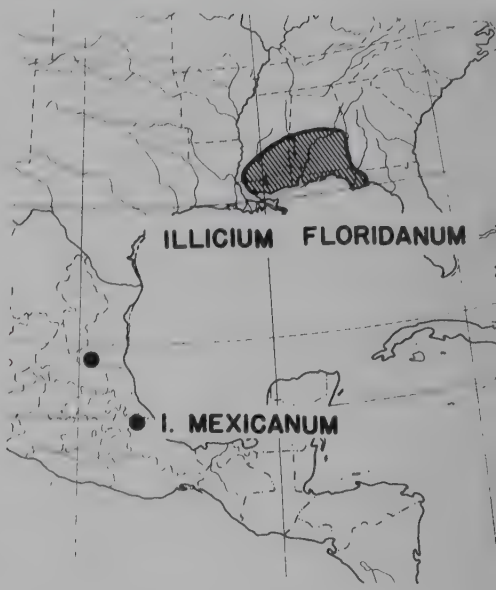

Fig. 8.

Figs. 1-8. Some temperate mesophytic trees and shrubs of disjunct distribution between eastern North America and Middle America. In Fig. 4 the range of *Fagus* is shaded, that of *Epifagus* is indicated by dots. Records of the latter from eastern North America are incomplete. In Fig. 5 the spots represent the distribution of *Acer skutchii* while the shaded portion of eastern North America includes the ranges of *A. saccharum, A. nigrum, A. barbatum (=A. floridanum)* and *A. leucoderme*. The range of *A. brachypterum* in northern Mexico is not shown.

Martin 1955a; Sharp *et al.* 1950). The biota of this area is known more intimately than that of any similar Mexican montane forest. Rancho del Cielo lies on the eastern slope of the Sierra Madre Oriental, latitude 23° 05′ north, longitude 99° 11′ west, about six kilometers north northwest of Gómez Farías at an elevation of 1070 meters. To our knowledge it is the northernmost outpost of oak-sweet gum Cloud Forest.

In the Rancho del Cielo flora 143 species of vascular plants have been identified (Harrell 1951; Sharp *et al.* 1950). Among the trees, the portion of the flora collected most thoroughly, forty-two are known (see Table I). Genera with the same or related species in eastern United States are marked with an asterisk, those which we consider as possible xero-mesophytes with a dagger.

Table 1

RANCHO DEL CIELO TREES COLLECTED AT ELEVATIONS BETWEEN 900 AND 1300 METERS. DATA LARGELY FROM HARRELL (1951)

Abies sp.
**Acer skutchii*
**Carpinus caroliniana*
**Carya (ovata* group)

†**Cercis canadensis*
Clethra macrophylla
†**Diospyros palmeri*
**Fagus mexicanus*
Fuchsia arborea
**Hamamelis* sp.
**Ilex* sp.
†**Juglans mollis*
**Liquidambar styraciflua*
Lonchocarpus sp.
**Magnolia schiedieana*
Mahonia chochoco
Meliosma alba
Meliosma sp. (close to *dentata)*
Sapindus saponaria
**Morus celtidifolia*
Parathesis sp.
Persea sp.
Pinus montezumae
P. patula
Podocarpus reichei
†**Prunus serotina*
Quercus germana
Q. rysophylla
Q. sierramadrensis
Q. sartorii
**Rhamnus caroliniana*
**Taxus globosa*
Ternstromia sp.
**Tilia* sp.
Trichilia havanensis
Turpinia occidentalis
Wimmeria sp.
(Five additional unidentified species)

* Genera with same or related species in eastern United States.
† Possible xero-mesophytes.

Excluding possible xero-mesophytes such as *Cercis* and *Prunus* which might have crossed south Texas in the Pleistocene *without following a forest corridor,* we have twelve strict mesophytes that appear to require continuous forest habitat for their establishment and survival. These twelve comprise 29 percent of the arboreal flora. On ten 100 square meter plots at Rancho del Cielo Harrell (1951) computed the mean basal area of all trees and large shrubs. The eastern temperate element comprises 4.57 square meters, or 23 percent of the total basal area of all trees in the sample plots. Thus this element is no less important in density (biomass) than in total percentage of the arboreal flora.

Regarding the vertebrate fauna, a different arrangement appears. Of 96 species of amphibians, reptiles, mammals, and breeding birds (fish are absent) collected in the Rancho del Cielo Cloud Forest (Martin 1955a) 90 do not occur in eastern United States. Most of the species present find their northern range limits in eastern Mexico south of 24° north latitude. Of the remaining six, three, *Ursus americanus* (black bear), *Didelphis marsupialis* (oppossum), and *Rana pipiens* (leopard frog), range almost continuously between eastern Mexico and eastern United States, or did so in pre-Columbian time. Their distribution is of no historical significance in the present problem. A fourth species in this region, the warbling vireo, is a member of the *leucophrys* group which is probably specifically distinct from the *gilvus* group including the form occurring in the eastern United States. Geographically, birds of the *gilvus* group approach the *leucophrys* group in soutwestern Mexico, where it is suspected that they overlap. If the two groups are conspecific, the relationship would be through the western cordilleras.

Two rather rare but distributionally significant species remain, *Storeria occipitomaculata* (red-bellied snake, Fig. 9) and *Glaucomys volans* (flying squirrel, Fig. 10). Both are found through eastern North America in temperate forests, reappearing in the Mexican escarpments. *Glaucomys* ranges south to Honduras, *Storeria occipitomaculata* no farther than Hidalgo in central Mexico. Although they appear to match the floristic pattern closely, their ranges are not well known. In any case the relative difference in the number of species at Rancho del Cielo with east-

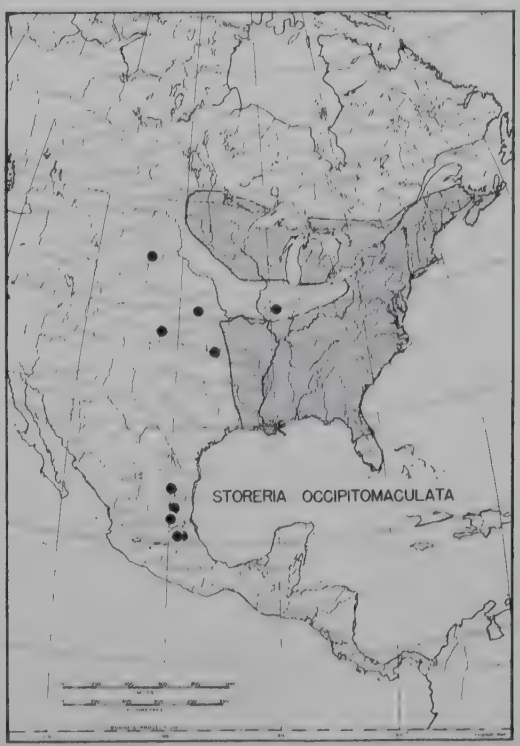

FIG. 9.

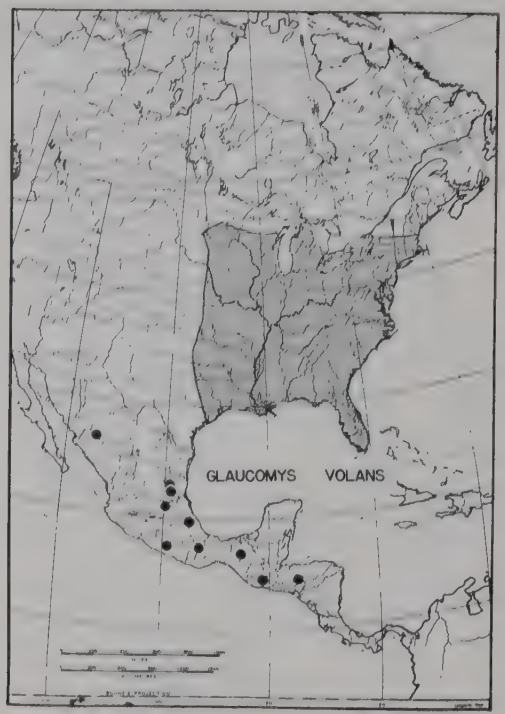

Fig. 10.

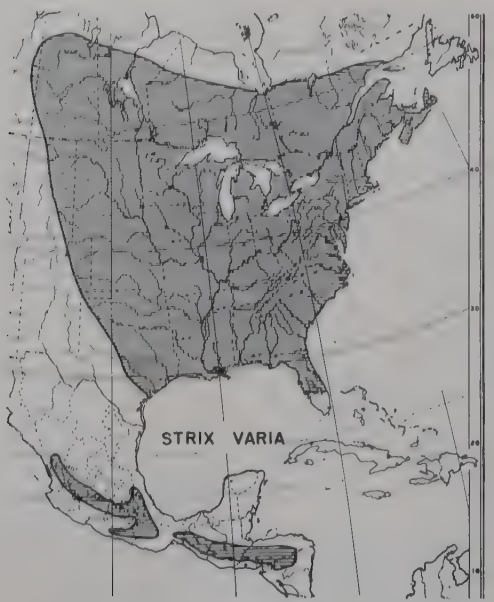

Fig. 11.

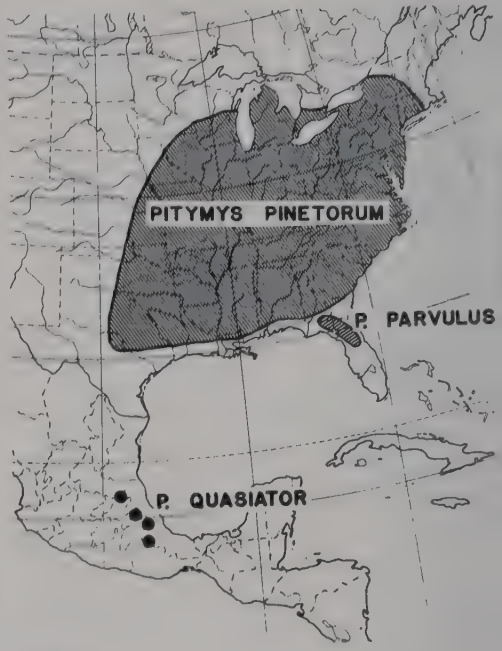

Fig. 12.

ern North American vicariads, two percent for the vertebrate fauna and 29 percent for the arboreal flora, does not provide impressive faunal confirmation of Pleistocene forest corridor to the northeast.

Montane Forest Faunal Relicts

To extend our search for possible Pleistocene relicts in the very rich fauna of montane forest environments, we will consider all such habitats in the Mexican and Central American Plateaus. Cloud Forest, Elfin Woodland, Humid Pine-Oak Forest, Dry Oak-Pine Woodland, and Fir Forest are among the vegetation types represented (see Fig. 14). We estimate that the total terrestrial vertebrate fauna in these habitats south to Nicaragua exceeds 775 species. Included are 265 birds, 200 mammals, 180 reptiles and 130 amphibians. Few of these occur in eastern North America. Even fewer occur *only* in eastern North America and the mountains of Middle America, matching the floristic pattern in question. In addition to *Glaucomys* and *Storeria occipitomaculata* mentioned above we are aware of only three other possible "fits" of the floristic pattern, as follows: *Rhadinaea laureata* (closely related to *R. flavilata*, the yellow-lipped snake of southeastern United States), *Strix varia* (the

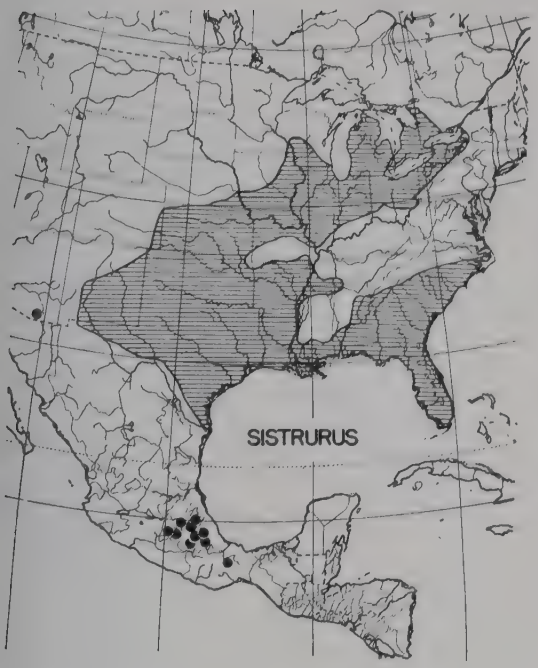

FIG. 13.

FIGS. 9-13. Distribution of five species of vertebrates inhabiting montane forests in Middle America. All are considered Pleistocene relicts. *Storeria* and *Glaucomys* (Figs. 9 and 10) parallel closely the floristic pattern; the other species range into prairie or savanna habitats in central Texas and elsewhere.

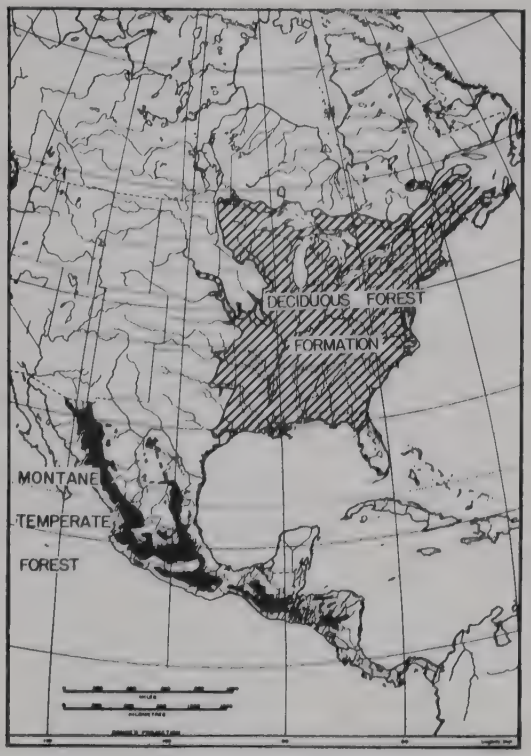

FIG. 14. Distribution of the Deciduous Forest Formation (from Braun 1950) in eastern North America and various temperate forests (Cloud Forest, Elfin Woodland, Oak-Pine Forest and Fir Forest) in the highlands of Mexico and Central America south to Nicaragua.

barred owl, Fig. 11), and *Pitymys quasiator*, related to *P. pinetorum* (the pine mouse, Fig. 12). Are these five examples from a fauna of 775 species sufficient to suport the postulate of a Pleistocene temperate forest corridor?

Because the ecological and geographical distribution of birds is better known than that of the other vertebrate groups, their distribution may be considered first. Presence of disjuncts might only reflect the dispersal potential of birds, but absence conversely should be of special importance. Approximately 200 species of land birds breed or formerly bred east of the Mississippi River in the United States and over 40% of these range into Mexico. However, nearly all of these have continuous breeding ranges through the arid habitats of Texas or through the temperate forests of western United States into Middle America. Only 14 species or superspecies have disjunct populations in eastern United States and in Mexico. Examining these in turn, we find that seven are found in the tropical lowlands of Mexico and in or near Florida in the United States; they represent an interesting Pleistocene problem but their history is not directly related to that of the temperate forests. *Aphelocoma coerulescens* and *Speotyto cunicularis* are widespread in western United States and in Mexico; in the east they both occur only in Florida, and in Mexico only *Aphelocoma* enters montane forests. *Elanus leucurus* is found in California, Texas, Florida, and the lowlands of Mexico south. *Cistothorus platensis* is found in the eastern United States and in marshes in the highlands of Mexico as well as in South America. *Vireo olivaceus* and *V. flavoviridis* (considered conspecific by some authors) and *Parula americana* and *P. pitiayumi* are two species pairs whose southern representatives live primarily in tropical rather than temperate habitats. All of these distributions are problems separate from ours. *Strix varia* (Fig. 11) is the only bird that has a disjunct range between deciduous forest of eastern United States and temperate forests of upland Mexico. In the Great Plains it ranges well out into the prairies

along wooded stream valleys and thus its distribution may parallel the xero-mesophytic element of the flora.

Although data on their distribution and ecological preferences are less complete, the reptiles, amphibians, and non-volant mammals are of equal and perhaps greater interest as associates of forest history than are the birds. We have mentioned four species or species pairs in the genera *Glaucomys, Pitymys, Rhadinaea* and *Storeria* which appear to fit closely the distribution of temperate forest habitats. Species pairs in *Sistrurus* (Fig. 13) and *Diadophis* (Blanchard 1942) are interesting disjuncts, but their habitat preferences do not restrict them to forest. While a closer relationship exists between temperate forest distribution and the modern ranges of *Glaucomys, Pitymys, Storeria occipitomaculata* and *Rhadinaea,* it is not necessarily obligate through time. Hibbard (1955: 83) has associated *Pitymys* with a late Pleistocene fauna including elephants, bison, *Cynomys* (prairie dog), and *Synaptomys* which ". . . must have grazed their way into Mexico at a time when strips or areas of grassland existed where semiarid conditions prevail today. The animals advanced with changing climatic conditions that supported the development of tall grasses or tall grasses and sedges." Can *Glaucomys, Storeria,* and *Rhadinaea* be added to this group? The ecological requirements and evolutionary history of these species appear too poorly known to insist that they provide faunal confirmation of a temperate Pleistocene forest corridor.

Lungless Salamanders and Cenozoic History

Rejecting the hypothesis of a Pleistocene connection, we may seek faunal evidence of a more ancient forest corridor to the north. The family Plethodontidae suggests such a relationship (Fig. 15). These lungless salamanders are concentrated in United States east of the hundreth meridian (13 genera, 42 species according to Schmidt 1953) and in Middle America (8 genera, at least 50 species). A much smaller number (five genera, 14 species) occurs in western North America, mainly west of the Continental Divide. Finding that the southern Appalachians are the center of maximum morphological and ecological diversity in the family, Dunn (1926: 11-12) concluded that this was its evolutionary center, an opinion that remains unchallenged.

While two of the five genera found west of the Rockies also occur in eastern North America *(Plethodon* and *Aneides),* none of the Middle American groups are regarded as congeneric with

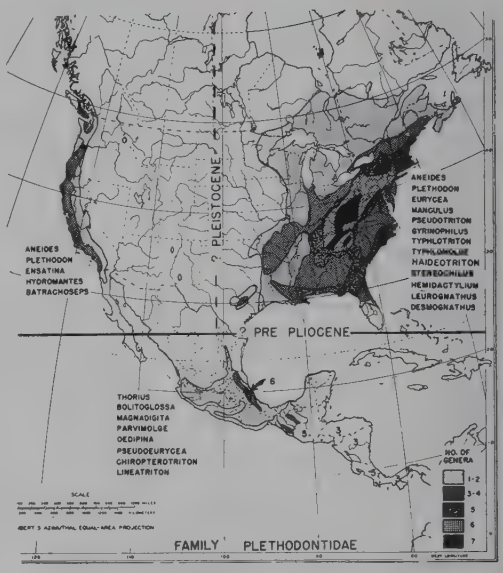

Fig. 15. Geographic centers of genera in the lungless salamanders, family Plethodontidae. No attempt was made at mapping generic density south of Mexico. Three centers of concentration, the genera present in each, and the inferred age of their most recent interconnection are shown.

those to the north (see Fig. 15). Tanner (1952) considers all the Middle American genera as monophyletic with distant affinity to the free-tongued salamanders of the *Gyrinophilus-Eurycea* line. Their nearest relative in this group is thought to be *Hydromantes,* a genus found both on the Pacific slope of the United States and in southern Europe. The possibility arises, therefore, that the Plethodontidae entered Mexico from western rather than eastern United States. On the other hand, Dunn (1926: 13) places the emigration as leading directly from Appalachia to Middle and South America, this in the late Miocene to Pliocene.

Whatever the location of the route, three considerations appear valid: (1) a continuous forest corridor is necessary for Plethodontid dispersal, (2) there is a closer relationship between the Plethodontidae in eastern and western United States, exemplified by *Aneides* and *Plethodon,* than between either of these areas and Middle America, and (3) the morphological development of the genera found south of the Mexican boundary requires the time of separation to antedate the Pleistocene. Certainly there is no evidence for an exchange of Plethodontid species between

eastern Mexico and the United States in the late Pleistocene.

Climatic Considerations

The hypothesis that eastern deciduous forest species withdraw to Mexico during the Pleistocene implies that this took place during a cool glacial period and that high latitude cooling was correlated with wet (pluvial) conditions in Mexico. Furthermore, it assumes that climatic change obliterated the present hot and dry barrier in south Texas and northeastern Mexico. A general correlate of this hypothesis is that the interglacials were dry and warm and that south Texas was as arid as it is today.

Unfortunately for such an interpretation, it is not yet possible to correlate low latitude pluvial periods with glacial maxima, although this has been attempted repeatedly (Deevey 1953). In fact, the opposite may be true. Radiocarbon dates of the Archaic Culture, associated with a high lake level in the Valley of Mexico, probably correspond not to a cool interval at high latitudes but to a thermal maximum, 5500-3500 B.P.* Our interpretation conflicts with that of Sears (1951) who places the Late Archaic-Teotihuacan transition in Xerothermic time, ca. 400-500 B.C. Actually in many high latitude localities the Thermal Maximum begins considerably in advance of this date. We note that the Late Archaic-Teotihuacan dry period is contemporaneous with glacial regeneration which began in Scandanavia about 500 B.C. (Ahlmann 1953: 41).

In any case the two major pluvial periods recorded in the Valley in the last 5000 years are too young to be associated with a major advance of Wisconsin ice (Table II). In addition Arellano (1953) suggests that the Barrilaco Pedocal, a buried caliche horizon, was formed about 7000 years ago under cool-dry conditions. This age estimate would correspond to that of the Cochrane readvance, 6500-7500 B.P. (Suess 1956). A correlation of these events indicates that recent high-latitude cool periods have been times of drought, not of abundant moisture, in the Valley of Mexico.

In an analysis of recent rainfall trends, Wallén (1955) draws some conclusions which would seem to support this correlation. He noted a decrease in summer precipitation, and therefore effectively in annual precipitation, in Mexico at a time of southward regression of the subtropical high pressure areas, the latter event correlating with the cooling in the north in recent years. The increase in precipitation must be associated with a northward shift of the subtropical high. Of course, extrapolating these observations to interpet glacial and interglacial climatic patterns is tentative, but at present it is easier to postulate a circulation system that would produce wet conditions in Mexico during the time of ice withdrawal than during the time of ice advance.

* B.P. Before Present.

Table II. Correlation of Wisconsin substages and climate in the valley of Mexico

North America		Valley of Mexico			
Glacial sequence	Age, BP	Horizon	Age, BP	C^{14} Sample	Climate
		Nahua	500-1100		warm-moist
		Teotihuacan	1100-2400		dry
		Late Archaic	2400-2600	C 200, C 202	
Thermal maximum	3500-5500	Archaic	2600-4500	C 196	warm-moist
		(unnamed)	5000	W 50	
Cochrane	6500-7500	Barrilaco Pedocal	ca. 7000	>C 198	cool-dry
Valders	10000-11000		11000	C 205	dry with moist fluctuations
Cary	13500-14500	Becerra	to over		
Tazewell	17000-18000	Superior	16000	C 204	

Sources: Arellano 1953, Libby 1955, Sears 1952, Sears and Clisby 1955, Suess 1954, 1956.

It is difficult to visualize a forest corridor through south Texas unless cool and moist conditions were correlated. If the rainfall were greater without a lowered temperature, tropical forests would extend northward and constitute a barrier to the disjunct temperate forests. If conditions were cooler but not more moist, Mexican temperate forests would descend the mountain slopes, but the arid barrier would remain. We suggest, therefore, that in the Pleistocene such a corridor did not develop.

Discussion

In challenging the hypothesis of Pleistocene arrival for certain mesophytes in the montane Mexican flora we emphasize that our objections do not extend to the biota of other habitats. To cite a very few examples, the relict distribution of *Ambystoma* in the Mexican Plateau, *Triturus (=Diemictylus)*, *Terrapene*, and *Ophisaurus* in the Gulf Coastal Plain and its foothills, *Cynomys* in southern Coahuila, fossil *Marmota* and *Synaptomys* in Nuevo León, and *Picea* pollen in the

Valley of Mexico appear related to important Pleistocene climatic change. However, the almost total absence in the montane forests of temperate faunal relicts from eastern United States is striking. It stands in marked contrast to the appreciable percentage of eastern North American trees and shrubs which reach low latitudes in these forests.

The possibility remains that some or perhaps all of the strict mesophytes spread across the arid Texas hiatus by accidental means not related to the profound climatic change necessary for the development of a forest corridor. At various times during a glacial maximum a cool oak-juniper, oak-pine, or possibly even pine-spruce savanna with tall grasses may have extended through south Texas into northern Mexico. The river valleys and arroyos running eastward to the Gulf of Mexico, presently either treeless, or bordered by gallery forest of *Sabal, Ulmus, Arundo, Celtis,* and *Fraxinus* as along the Rio Grande (Clover 1937: 82), were swollen by increased runoff. Under such circumstances some mesophytes including *Fagus, Acer, Liquidambar,* and *Carpinus* might have occupied the enlarged flood plains. The formation of "resacas" or ox-bows would facilitate habitat-hopping from one drainage to the next. Certain mesophytes could thus extend their ranges into (or out of) Mexico along a route obviously more suitable to plants than to animals.

Such a system we consider of questionable effectiveness for three reasons. First, many of the plants involved such as *Liquidambar, Magnolia, Hamamelis, Mitchella, Fagus,* and *Nyssa* have diaspores not well suited to wind or animal transport, even across short barriers. Second, unstable flood plain habitats would not appear suitable for certain upland species including *Carya (ovata* group), *Pinus strobus,* and *Taxus globosa.* Third, and most critical, any individual accidentally spreading either north or south along this route would have to penetrate a well established native flora in either Mexico or eastern United States.

As the most satisfactory working hypothesis we propose that the majority of the Arcto-Tertiary mesophytes reached the montane Mexican forest by the mid-Cenozoic at the latest. A faunal parallel to this floristic interpretation is evident in the distribution of the Plethodontidae.

During the Pleistocene there was probably additional biotic exchange with eastern United States along a savanna or prairie-border woodland through northeastern Mexico and Texas. This ecological bridge permitted such xero-mesophytes as *Cercis, Juniperus, Prunus serotina, Juglans,* and *Carya pecan* to re-establish contact. At this time certain animals including *Glaucomys, Pitymys, Sorex cinereus, Strix varia, Ophisaurus, Coluber, Storeria occipitomaculata, Sistrurus,* and *Diadophis* entered (or left!) the Mexican Plateau. Subsequently some of these, e.g. *Storeria,* spread into montane forests of the Plateau escarpments while others such as *Coluber* remained exclusively savanna relicts.

The biogeographic theory interpreting present distributions entirely in terms of Pleistocene conditions raises many problems that do not exist if earlier as well as Pleistocene events are considered.

In effect our biogeographic and climatic interpretation makes a choice between Deevey's alternatives (1949: 1395): ". . . whether the desert barrier that now opposes the southward migration of north-temperate organisms was obliterated during the Pleistocene, or merely somewhat debilitated." If humid montane faunas are a suitable index, the arid barrier was not obliterated.

Summary

1. The montane flora of Mexico has a marked affinity to the flora of the eastern United States. This affinity has been explained in two ways. It has been suggested that the mountains of eastern Mexico became a refugium for retreating eastern temperate forests during the height of a glacial period. The opposing theory states that the temperate element had reached Mexico by the mid-Cenozoic and became disjunct from its northern counterparts by the Pliocene development of an arid zone in southern Texas and northeastern Mexico. In the Pleistocene the arid zone ameliorated only enough to allow passage of those temperate animals and plants that could exist under savanna conditions.

2. The eastern North American element in the humid montane fauna of Mexico is much smaller than that evident in the flora. At one station in northeastern Mexico this element comprised 29 percent of the arboreal flora and two percent of the vertebrate fauna.

3. Of a total of 775 terrestrial vertebrate species inhabiting temperate forests of Mexico and northern Central America only five are disjunct representatives of species confined elsewhere to eastern United States.

4. Present evidence thus suggests that few temperate-forest animals were able to cross the arid Texan barrier in the Pleistocene. These probably did so along a cool savanna or open woodland corridor.

5. Salamanders of the family Plethodontidae provide faunal confirmation of a pre-Pleistocene (mid-Cenozoic) arrival of warm-temperate animals in Middle America. Presumably this was no later than the arrival of the Arcto-Tertiary flora and the establishment of separate populations of sweet gum, hard maple, beech, evergreen magnolia, etc. in eastern United States and in Middle America.

6. Climatic conditions postulated for northeastern Mexico include persistence of an arid barrier separating eastern North American from humid montane Mexican biotas through the Pleistocene. Although pluvial periods occurred in this region, they may not have been in phase with glacial maxima.

7. Interpreting the eastern temperate (Arcto-Tertiary) element in the Mexican montane biota exclusively in terms of Pleistocene dispersal raises more distributional problems than it solves. An earlier (pre-Pliocene) arrival of temperate plants and lungless salamanders appears more in accord with present evidence.

Acknowledgments. R. M. Dressler of the Gray Herbarium generously presented us with the distribution maps employed in Figs. 4, 6, 7, 8, and 12. For their comments we are especially indebted to J. R. Borchert, E. S. Deevey, Jr., R. M. Dressler, E. Hernández X., D. B. Lawrence, A. J. Sharp, C. F. Walker, D. W. Warner, and H. E. Wright, Jr. This paper was completed while Martin held a Rackham Postdoctoral Fellowship from the University of Michigan.

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FUNGUS-GROWING ANTS AND THEIR FUNGI: *CYPHOMYRMEX COSTATUS*

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The present study is one of a series of investigations into the factors responsible for the production and maintenance of thriving cultures of fungi in ant gardens despite continual possibilities for contamination (Weber 1955, 1956a, b). It is the first study which resulted in the development from artificial culture of the sporophore or fruiting stage of the ant fungus, a necessary step in ascertaining the identity of the fungus. In the present account, Part I consists of the observations and experiments on the ant colonies and gardens, followed by similar data on the subcolonies. The fungus itself is considered in Part II, including its cultures, verification of these as true ant fungi and the production of sporophores.

The colonies and cultures were gathered in the Panama Canal Zone, with the assistance of Swarthmore College and the American Philosophical Society. Through the aid of the Joseph Henry Fund of the National Academy of Science and the National Science Foundation they were studied on sabbatical leave from Swarthmore in the Department of Bacteriology, University of Wisconsin. It is a pleasure to acknowledge the many courtesies and assistance of the staff of the Bacteriology Department and especially of Professors K. B. Raper and W. B. Sarles, and of Professor M. P. Backus in the Botany Department.

PART I

DISTRIBUTION AND APPEARANCE OF THE ANTS

One of the smallest fungus-growing ants is *Cyphomyrmex costatus,* described by Dr. W. M. Mann (Mann 1922) from three workers which he took at Lombardia, Honduras in rotted wood. The general biology was later described (Weber 1940, 1941) from Barro Colorado Island, Panama Canal Zone. A guest ant living with it, *Megalomyrmex (Cepobroticus) wheeleri,* was described as the second such relationship in the Attini.

The ants are common on Barro Colorado Island, nesting in the forest under rocks or under rotted wood in the soil, and were also common at an elevation of abut 1,500 feet on Cerro Campana in western Panama some 50 miles from Panama City, where they occurred under rocks in grassy areas. The nest consists of an elliptical cell in the soil with the long axis horizontal and contains a garden some 30 x 20 mm that has a height of about 10 mm; younger nests have of course smaller gardens and some older gardens may be larger. There are generally less than one hundred workers in a mature colony, and the winged sexual forms may remain in the nest for weeks. The brood is so heavily swathed in the mycelium as to be easily overlooked. A peculiarity is the universal use of parts of the empty carcasses of

other arthropods, most frequently other species of ants, in the gardens as supports for the substrate. Remains of such arboreal ants as Pseudomyrmex, Cephalotes, Cyathomyrmex, Azteca, and Camponotus are easily recognized and terrestrial genera include Ectatomma, Odontomachus, Ponera, Neivamyrmex, and Pheidole. These fungus-growers have not been seen to climb trees and must pick the carcasses from the forest floor.

The worker ants (Fig. 1) are about two millimeters long, with a thorax length of 0.7 mm, and have a pair of longitudinal mid-dorsal carinae, the latter character separating them from all but several South American species of this large genus. The prosternites are covered with a white bloom. The sexual forms have long wings (2.2 mm in the female, 2.0 mm in the male) which extend back of the body so that as they crawl in life the female is about 3.4 mm (thorax 0.8 mm) and the male about 2.9 mm in length (thorax 0.8 mm). The latter has mid-dorsal gastric carinae faintly indicated and has strong lateral carinae here. The female has gastric carinae as in the worker.

Material Used

Four colonies were used in the present study, all from Barro Colorado Island and collected June 25-27, 1955. These are referred to below for convenience as Colonies A, B, C, and D. Colony A produced the first sporophores. An artificial culture of the fungus of Colony B resulting in sporophores was also obtained. A few ants or garden fragments from the colonies were removed for short experiments or mingled in other combinations and are referred to as Sub-colonies E—I.

Of the four nests, two were under rocks in reddish clay soil, one was under a log and the fourth was in clay under an active crater of *Atta cephalotes isthmicola*. One of the rock colonies nested with small colonies of other small ants of Ponera, Pheidole and Strumigenys within an area having a diameter of 25 cm. The Ponera nested in the center and had numerous galleries, the Pheidole was a smaller ant with tiny galleries interdigitating with those of Ponera and the Strumigenys and Cyphomyrmex nests were more peripheral. The substrate in one *Cyphomyrmex costatus* nest consisted entirely of golden brown cylindrical particles, mostly 2-3 mm long and about ⅔ mm in diameter, apparently from large fruits being dropped by monkeys in the high trees overhead.

The substrate regularly made available to the ants for their gardens was a cassava starch preparation imported from South America in the form of coarse granules. This is hereafter referred to as cassava granules.

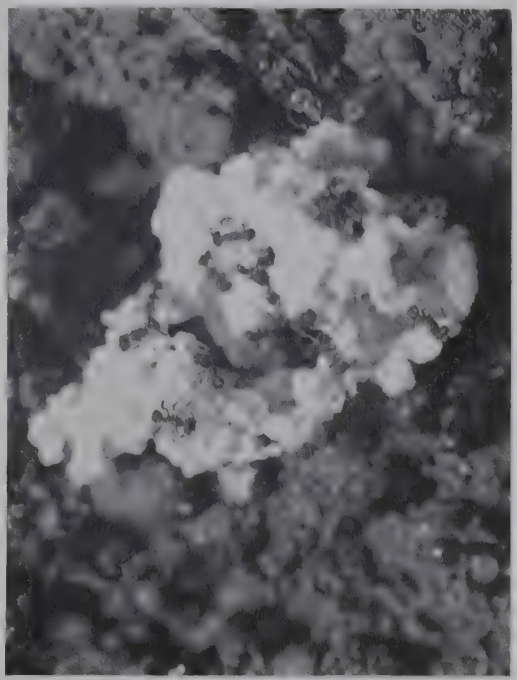

Fig. 1. The observation nest of Colony A of *Cyphomyrmex costatus* on January 11, 1956. The ants as shown here are about 1.8 mm long. The fungus is growing as a velvety mycelium of short, upright hyphae on white cassava granules for substrate.

Colony A (Fig. 1)

On June 25th the ants and garden of Colony A were placed in a Petri dish* in the field, the garden crumbling as it was collected. Overnight it was rebuilt to normal appearance. Four potato-dextrose-agar tubes were then inoculated with the fungus. By July 16, after transfer from Panama to Pennsylvania, the garden was about 55 x 20 mm in lateral diameters and approximately 3 cc in bulk. On July 30 the colony was placed in a larger observation nest that contained a colony of *Apterostigma angulatum*, where it remained until January 5.

During August the garden became smaller (about 2 cc on the 28th) and some of the ants escaped under the loose cover. By the 19th the ants had built walls of clay around the garden and these were perfected during September, after transfer of the colony to Wisconsin. The resulting elliptical cell had an internal diameter of 22 x 16 mm and a depth of 10-13 mm. The glass cover was used as the roof and the walls were 2-5 mm thick. Dead rootlets permeating the area were retained as a support for the garden.

In October the ants moved the garden out of this cell into the clay soil which largely filled part of the

* (15 x 100 mm here, and where petri dishes subsequently were used.)

observation nest. A lens-shaped cavity was excavated that was difficult to see since only part of a side was visible. The garden was estimated to be about one cubic centimeter in bulk on the 7th and alate ants, apparently male, were present.

The colony and garden were moved to a Petri dish container on January 5, 1956, when the garden was an estimated 1 ½ cc. A callow male of pale color, instead of the black of the adult, appeared on January 20. One of comparable coloration had appeared on January 14 in Sub-colony I and it is probable that both emerged from the pupal state at about the same time. Two callow males of different ages, as shown by their coloration, were in view on the 23rd and four on the 30th. Five males were glimpsed on several occasions during February, including one that was not over a day old, and six at one time on March 2. There were then two large larvae, probably also male. Recent callow males were present on April 11 and on May 1 and were the last brood to mature.

The garden fluctuated in bulk, increasing from substrate or cultures furnished them that are detailed elsewhere to a maximum of about 2 ½ cc and decreasing to about $\frac{1}{10}$ cc by the end of April. The deterioration was probably due to the infestation of mites and Collembola (*Cyphoderus inaequalis,* determined by Dr. Kenneth Christiansen).

A luxuriant growth of their own fungus cultured since January 25 on Sabouraud's agar was introduced on May 1. Seven minutes later an ant was actively cutting the uneven, floccose, white mycelium and was then joined by two other ants. They carried the fungus back to their vestigial garden that now consisted of two fragments, one about 2 x 2 x 2 mm, the other not over 6 x 2 x 2 mm in maximum diameters. Later in the day nine ants were cutting the cultured fungus. The colony was not thriving by the 18th and was transferred to another nest with sterile sand. Four workers and two males were dead and piled together. At least five males were alive on the 19th and the colony was again flourishing on the 26th. When they were given a small part of a gill of a recently produced sporophore from Colony B they ignored it, remaining on the older cultured fungus of May 1.

By June 2 this artificial culture had taken on the same appearance as a normal garden, due to the manipulation of the ants, and consisted of irregular tufts of the mycelium on its original agar base. The ants had removed some of the tufts and formed a small pile on wet sand that was about 10 x 20 mm. No ants could remain unseen and the male population was clearly six. There was no female. Within two days, however, a sudden deterioration took place. The small pile of fungus on wet sand now had minute nematode worms active in it. The ants had removed another small mass of fungus from the artificial culture to a site on the sand 30 mm distant. Some were in attendance here and some were on the old culture. An odor of decomposition was present in the container the next day although the old agar base of the fungus seemed normal. The ants were moved to a new container. Five males and seven workers at this time constituted the living ant population. The males died during June and the last workers died in early July.

Colony A thus had a life in captivity of a year during which a maximum bulk of the garden of about 3 cc was attained. The garden fluctuated markedly in bulk and was variably infested by collembolans, mites and nematodes. Males were present in the nest as early as October 7 and others matured from January to April. Since no female was observed in the nest it is probable that workers laid the eggs that developed into the males. The larger attines have an incubation period of about two months (Autuori 1942; Weber 1956a) and it is therefore likely that eggs were laid at various times during the year.

Colony B

Colony B was collected on June 27. The ants built up their garden overnight and this fungus was used for inoculating potato-dextrose tubes in the morning. The substrate was mostly a golden brown color and the garden appeared gray on the outside from the fungus growth. The garden increased in estimated bulk from about 2 cc on July 13 to about 3 ½ cc on September 23. On the latter date a callow female was emerging from the pupal state and there were many larvae, all coated with mycelium.

The garden bulk was about 2 ⅓ cc on January 6 and about 2 cc on the 30th. From a low of about 1 ½ cc on February 10 it grew in a month to about 2 ⅕ cc, then dropped to about 1 ½ cc on March 13, probably because of mites and a bad infestation with the collembolan *Cyphoderus inaequalis.* Cultures of *costatus* fungi were given to resuscitate it, as detailed elsewhere.

Males were visible in the nest on October 13 and both winged sexes were present from November until shortly before the colony was ended in the following July. Seven males were in view at once on January 12, the maximum male population that was seen at one time. A maximum of eight alate females was attained. Workers were also produced in the colony, one new callow appearing on March 13. By June 5 the total adult population consisted of eight alate females, three males and 17 workers; later in the month several females lost their wings. When observations were terminated on July 2 there were three alate and two dealate females and three workers alive.

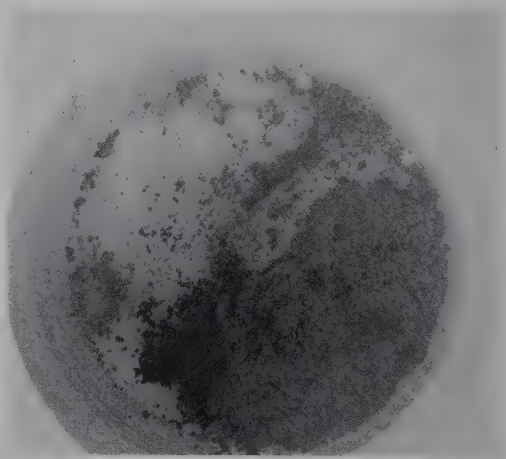

Fig. 2. Colony C in a Petri dish on June 29, 1955 two days after it was collected. At this time only the ant's natural substrate had been used. A rule with the metric scale shows through the glass.

Colony C (Fig. 2)

Colony C, originally from clay under the crater entrance to a colony of *Atta cephalotes isthmicola,* had a

garden in two parts totalling about 3 cc on July 13. By the end of August it was half this size and on October 6 alate males and females were present. The colony was placed in a four-gallon glass jar with clean sand that contained a colony of *Trachymymex cornetzi gatun* on October 10. The ants were free to nest anywhere in the jar but remained in their original Petri dish nest, although foraging freely, until January 5 when the ants and their garden were removed to a clean Petri dish. By this time the garden was about ¾ cc in bulk. The ants were given dyed cassava granules and cultured fungus of Colony A, as detailed elsewhere, and maintained a garden of comparable bulk through February.

While the nest was being observed on March 9, prior to moving it again because of a heavy *Cyphoderus inaequalis* infestation, a small brown spider ran about, then disappeared down a hole in the sand. It immediately emerged, carrying a live *Cyphoderus*. Later a second female spider was seen and both were determined as *Triaeris patellaris* Bryant (Onoopidae) by H. W. Levi. The presence of eight recently dead ants indicated that the spiders had been preying on ants as well as collembolans. Since this species of spider and the group to which it belongs are known only from Panama it is probable that they were collected originally with the ants.

Cassava granules were added after the change to a new Petri dish and by the next morning a particle, about 1 x 2 mm, had been incorporated into the garden. It contained more than 14 tiny mycelial tufts, widely scattered and with no connections between them, thus indicating that they had been planted by the ants. Other new granules had similar tufts.

The garden grew to about 1 cc by March 27. The colony was transferred on April 30 to sterile clay in a new container to get rid of some of the infesting mites and collembolans. By the end of May the garden was in poor condition and about ⅝ cc. A dealate female and 10 workers were dead; one feeble dealate female and two workers remained alive. The colony was terminated on June 2, one worker and a vestigial garden remaining.

Colony D

Colony D, the colony that nested in the midst of other small ants, was placed in a 19 x 150 mm test tube in the field. The garden was an estimated 2 ½ cc in bulk on July 13 and an alate female was seen on August 3. The colony was kept primarily as a source of material for experiments that are mostly detailed elsewhere.

Some of the garden and a few of the ants were placed in a Petri dish of sterile Sabouraud's dextrose agar on August 3rd and two days later (26° ± 1° C in the interval) bacterial or alien fungal colonies covered much of the agar surface except at the side of the garden. The ants excavated a little agar at one side. Some of their garden substrate was discarded, the remainder having a normal ant fungus growth. By the next day alien fungi were developing on the abandoned substrate and they and bacteria were encroaching on the garden.

The garden was about 1 cc at the end of August. During the first half of September the tube was in a room that often had a temperature of 30° C. Despite the high temperatures in September the ants maintained a garden with a moderately dense mycelium. Several alate females and the workers appeared unusually active in their movements.

The ants were given access to a tube of a culture of Colony A fungus on potato-dextrose agar on December 16 and within 11 days had worked over it considerably although without developing a garden here. When this tube was removed on January 3 (21-25° C in the interval) there was no obvious contamination such as might normally occur in the absence of this ant fungus. During the period the ants had been crawling over the agar surface frequently and had removed the fungus except for scattered strands of hyphae.

The colony was removed to a Petri dish from the tube on January 5, when 25 workers and three alate females could be seen and the garden was about ½ cc. A few minute white millipeds and many of the white Cyphoderus collembolans had been living in the original Panama clay. By January 20 the millipeds had grown to 3-4 mm and two were removed, a worker first exhibiting hostility to one. The garden doubled in size during the month but was reduced to about ½ cc on March 9 when the colony was again moved to a new container to get rid of as many infesting *Cyphoderus* as possible. The garden doubled in size during March but was decreasing by the end of April when the colony was once more moved.

A newly emerged callow male, pale yellow brown in color, appeared on May 21. It had been glimpsed as a larva on March 9. By the end of May two larvae coated with mycelium and alate and dealate females could be seen. One of the larvae was a pre-pupa on June 5 and was still covered with the mycelium; by the 13th it had become a male pupa, clean, shiny and lacking any pigment. All members of the colony were dead by June 20, the male pupa having faintly gray eyes.

Sub-Colonies

A few ants and small fragments of gardens of Colonies A-D were removed on January 13, 1956 and re-combined in Petri dishes on sterile clay to form Sub-colonies E-I as follows:

Sub-colony E consisted of a male, two workers, and a fragment of the garden of Colony B, together with an alate female of Colony D.
Sub-Colony F consisted of a male, one worker and a fragment of the garden of Colony B, together with an alate female of Colony C.
Sub-colony G consisted of an alate female, two workers and a fragment of the garden of Colony B.
Sub-colony H consisted of an alate female, seven workers and a fragment of Colony A.
Sub-colony I consisted of four workers of Colony D and a fragment of the garden of Colony A.

The ants of these new combinations were compatible, and the ants of one colony accepted a garden fragment of another as was found to be the case in *Trachymyrmex septentrionalis* and *T. seminole* (Weber 1956 a, b). Six hours later on the 13th all were given tufts of the artificially cultivated mycelium from Colony A that had been growing on a wood block.

The next day this fungus was found to have been clearly adopted by four of these nests, in three of the cases to the neglect of their original garden. Three of the alate females were tending the tufts as did the workers. The male in E was being bound in the web of a very small spider but was released. Sub-colony I had a newly emerged pale brownish-yellow callow male with wings still unexpanded. It had inadvertently been transferred in the pupal state as an apparent fragment of garden. Past experience with some species had demonstrated that the swathing of brood in mycelium frequently rendered them indistinguishable from parts of the

garden. The other males were the normal black in color.

By the 15th one female had lost all of her wings, one female had lost all but a single hind wing and the callow male's wings were still crumpled. On January 16 the winged forms were as before except that the callow male's wings were partially opened and the ant was darkening.

Later in the month the females lost their wings and the two adult males died. The callow male of Sub-colony I slowly darkened to a brown color by January 30 and was black at the time of its death through desiccation on May 21. The ants of Sub-colony H were dead by February 3, probably through injury; Sub-colony E was terminated on February 20. The female of F lived to June 4, that of G to June 10, and during the nearly five months interval neither was observed to lay eggs.

The sub-colonies were particularly useful for testing reactions to the sporophores, as described in Part II.

Behavior of the Ants

A habit of *Cyphomyrmex costatus* that has not regularly been observed in other attines is that of "jigging." In this performance the ant stands in one place on the garden, usually with the last four legs on it, and jigs up and down in a vertical plane with the rest of the body and the fore legs. The stimuli eliciting this behavior appear to be those of disturbance, *e.g.* the sudden appearance of light in a darkened nest, jarring of the container, or motions of one's fingers within several centimeters of the glass cover. It may last for a variable fraction of a minute and several ants may act at the same time while others nearby with the same exposure may not react in this manner.

The thorough licking of the body and appendages is a feature of *C. costatus* as in other attines. Several may groom one ant, which remains stationary during the process, and this treatment may be extended to the winged forms of both sexes, the grooming including their wings and antennae.

Their reactions to their own and to other fungi and their treatment of substrate are detailed separately.

Substrate and Its Treatment

In addition to the cassava granules that were regularly supplied, the ants used other substrate. The ants, when supplied with whole rose flowers, took the stamens, carrying them to the garden and defecating on them. They were then planted with tufts of the mycelium.

The ants of the *costatus* colonies also planted tufts of the mycelium at various times on rounded quartz sand grains that were orginally introduced into the containers to hold moisture. They took these grains to the garden, where they were incorporated as substrate. This was similar to the use in nature of apparently inert skeletons of insects.

Dried fecal pellets of the caterpillars of the Monarch butterfly *(Danaus plexippus)* and the Viceroy *(Limenitis archippus)* were sent from Florida by Lincoln Brower and were given to the ants in May, 1956. The caterpillars of the Monarch, distasteful to birds, had been feeding only on *Asclepias humistrata;* those of the Viceroy, tasteful to birds, fed on *Salix* spp.

Two of each type of fecal pellets were placed in the nest of Colony B on May 17.

Four hours later one of the *Limenitis* feces had been dragged 2 cm to a site on bare clay, the others remaining where they were originally placed. Two days later one of the *Danaus* feces had been broken up into its coarse plant sections and many of these were embedded in the garden. Already (23-26° C in the interval) they were bearing luxuriant fungal growths. One *Limenitis* fecal pellet was being licked in many places for several minutes by an ant. The ant also tugged briefly at a small tuft of an alien fungus growing on it but without removing the growth. The reactions of these ants in licking the caterpillar feces, breaking them up into their leafy pieces and incorporating them into the garden were exactly comparable with the treatment given to the feces of these two caterpillars by *Cyphomyrmex rimosus,* Trachymyrmex, and Acromyrmex at the same time. By the 21st some of the fungus on the caterpillar feces was of the densest type and the general growth was normal. When colonies were given these caterpillar feces on other occasions they were not used.

Use of Dyed Substrate

In order to follow the history of individual pieces of substrate, they were dyed red with Neutral Red or black with Nigrosin, then dried and placed before the ants.

In one experiment with Colony A such dyed cassava granules were given to the ants on January 6. One of each color was placed on the garden itself. Within seven minutes several ants had approached the black particle momentarily, exploring briefly with the antennal tips and then recoiling as though the material were distasteful. After six more minutes an ant felt the red granule with antennal tips, then removed it to an invisible site. Two hours later there were 22 discrete tufts of hyphae on the black particle (24.5° C in the interval) and under 27x magnification of the microscope it was clear that the tufts were independent of one another and with collapsed hyphae so that they could not possibly have ar-

rived there except through the agency of the ants. In experiments with other species the actual transfer has been observed.

This particle was held on the garden by three pieces of fungus-covered substrate that barely touched it, and from none of these did hyphae extend onto it. There was no further change within the next hour. On the following morning the black particle had the same tufts in a growing condition with some hyphae extending upright (24° C in the interval). It was partly concealed from above by a normal particle of the garden. Seven and one-half hours later the tufts showed further growth and the adjacent particle was taking up the dye. By January 8 the black dye had spread to two uncolored cassava granules and all, including that which was dyed, were growing the fungus normally. This was also true on the following three days (23-25° C in the interval). The garden was photographed (Fig. 1) on the 11th with glass cover momentarily removed. On the 12th the cassava granule which had absorbed dye appeared to have a shorter growth of hyphae than older granules.

In other experiments with the colonies the ants regularly accepted either the red or the black dyed granules and incorporated them into the garden, planting tufts of mycelium on them. Colony D ants once accepted five of eight red granules. One had eight isolated mycelial tufts planted on a surface less than 2 mm long, a second granule received 11 tufts on a surface less than ½ mm in diameter and a third had six tufts, all within 22 hours at 24-25° C. The other two accepted granules were freshly embedded in the garden and had not yet received any tufts.

Substrate with Yeast Extract

In an attempt to increase the rate of growth of the gardens, the cassava granules furnished to the ants on several occasions were first dusted with Difco dried yeast extract containing the Vitamin B complex. Colony A ants, given them on February 10, accepted these and within nineteen hours at 23-25° C nearly all had been incorporated into the garden. Already they bore many isolated and minute tufts of the mycelium that had been planted by the ants. The garden flourished and increased to an estimated bulk of 2 cc on the 17th from an estimated bulk of 1 ⅔ cc, due entirely to the treated granules. By the 20th, however, the bulk was reduced to about 1 ½ cc and more treated granules were introduced, with the result that four days later the bulk was again about 2 cc. A complicating factor was a bad infestation of the white collembolan *Cyphoderus inaequalis*. A maximum bulk of about 2 ½ cc was reached by April 27.

Similarly dusted granules were used by other colonies. The females of Sub-colonies E and F added these to gardens consisting in part of a stipe section of a sporophore (see Part II) and the granules bore tufts of hyphae planted by the ants.

Instead of being given dusted granules of substrate, the yeast extract powder was added directly to the garden of Sub-colony G. Within an hour the female was removing those parts of the garden which lacked the, by now liquefied, yeast extract. The worker did not participate in this action. The female made several quick, biting attempts at a clear yeast globule. She placed her fore feet on it several times without penetrating the surface film, then appressed her mouthparts and in about 30 seconds, imbibed nearly all of the contents. More was absorbed three minutes later before she pulled out a tuft of fungus. She soon returned and took another droplet as before. Five days later dusted granules were given to the ants, the garden being maintained in a flourishing condition, and all were taken into the garden.

Reactions to Other Ant Fungi

Cultured fungi from their own species were given to the ants as detailed elsewhere. They were also given the cultured fungi taken from the gardens of other genera of ants. For example, on January 6, 1956 the ants of Colony B were given a tuft of the cultured fungus from a colony of *Apterostigma mayri*. It was placed on the garden so that it rested on the *C. costatus* fungus itself. The ants came up immediately, waving their antennae toward it. The alien fungus consisted of long, thin hyphae with clamp connections, and therefore Basidiomycete, that always collapsed on the inoculating needle and these stuck to the *costatus* fungus. Five minutes later an ant almost touched the alien fungus, then recoiled. The hyphae of the fungi when so brought together appeared of the same degree of fineness and were indistinguishable under the low-power binocular microscope except in length. Fourteen minutes later an ant approached, felt the alien fungus with its antennae and started pulling the tuft away. Four other ants came to the immediate vicinity but started feeling their own fungus. After two minutes, two of these pulled on another part of the tuft and two minutes later one ant pulled the entire mass, including a large pellet of its own garden, away to one side. Here it touched condensed moisture on the glass ceiling that made the task harder but it kept at

work. After four minutes the ant was attempting to take it down a hole in the soil 8 mm distant, where it came to rest. Three ants stayed behind and examined the disrupted part of the garden. The one ant remained at its task of moving. A large, brown mite was eating the fungus six minutes later. The following morning the alien fungus was not in sight and all pellets of the normal garden were in place and flourishing. The alien fungus was not seen on subsquent days and, since there was no unusual contamination it could well have been consumed by a number of the brown mites that were present.

In another experiment ants from Colony D were removed on August 13. They were deprived of food until the next day and then given a culture of the fungus of *Trachymyrmex septentrionalis seminole*. Within half an hour two of the ants were pulling out tufts of the hyphae and eating them. Other ants were given a culture of the yeast-like fungus of *Cyphomyrmex rimosus* but did not react to it within an hour. Within two days, however, they had cut out bromatia-size particles (¼-½ mm) and piled them on the remainder. They also cut agar blocks but there was no evidence of their eating the fungus.

The same ants were placed in a tube of the cultured fungus of *Acromyrmex octospinosus* on August 17 and by the following day had eaten much of it. The remainder of the hyphae were built up into a garden and an ant was seen to eat them. Most of the culture had been removed from its agar base and the part left was normal in appearance.

Five ants of Colonies B, C and D were isolated from their nests and placed together. Six hours later two were given the artificially cultured fungus (lacking any agar base) of a colony of *Mycocepurus tardus*. Two minutes later one ant explored it briefly and after two minutes the second ant touched it with the antennal apices, then started feeding delicately, opening and shutting the mandibles slightly while the other mouthparts were used for feeding. It fed continuously for three minutes, then raised up, cleaned its antennal apices through the pectens of the fore legs and cleaned the fore legs themselves alternately in the same manner. Finally it combed its right hind leg through a fore leg pecten and went off. Soon the other ant explored the fungus briefly and crawled over it without tasting.

The remaining three ants were given a small amount of the artificially cultured fungus (without any agar base) of *Acromyrmex octospinosus*. One tasted it briefly two minutes later, then went off, only to return in less than a minute to commence feeding intently on it for nearly three minutes. It then cleaned its antennae and fore feet and returned to feed for an additional minute.

Both lots of ants had some fungi left the next day but all were dead after four days, some fungi remaining.

When a small amount of the cultured fungus of *Trachymyrmex septentrionalis* was placed 6 mm from the garden of the female of Sub-colony E she did not at first discover it. Within 16 minutes, however, she became aware of it and pulled the fungus away to a distance of 21 mm, where it remained ignored. A mass of bromatia from the same Trachymyrmex culture was placed on the garden in Sub-colony I. Within a minute three ants explored it indecisively with their antennae, then went away to clean these briefly. Soon another ant came up and tasted the fungus, then went away to clean these briefly. Another ant approached and tasted the fungus, then a different one ate it intermittently for fully one minute, repeating this feeding after an interval of a minute. Ten minutes after the fungus was introduced a worker ant cut out a portion that was half the size of its head and carried this directly to the sporophore stipe section (see Part II) that was being used in the garden. The ant placed the alien fungus firmly on top of the stipe section where hyphae were proliferating in tuft form. It then returned to the main part of the alien fungus and took another fragment, placing this at one side of the garden. The male ant appeared to taste or sense it intently without moving for some seconds. The one ant that had fed earlier returned and steadily ate the *Trachymyrmex* fungus for over three minutes, repeating the performance later for an additional two minutes. The alien fungus was not recognizable three days later.

PART II

Culturing the Fungus

Cultures of the fungus of Colonies A and B were first made during the morning following the collection of the colonies. By this time the ants had rebuilt their gardens to normal appearance. Potato-dextrose agar tubes of Colony A fungus were inoculated on June 26, 1955 and similar tubes of Colony B fungus on June 28. An additional culture of the latter was secured on June 30 by taking cassava granules dyed red with Neutral Red, then dried, that had been given to the ants the evening before. By the next morning the ants had planted tufts of fungus on the granules that, upon inoculation on agar, resulted in the same type of growth as in the other two.

A similar type of culture had been temporarily maintained the year before from other *C. costatus* colonies.

From the beginning, the cultures differed markedly from those of *Cyphomyrmex rimosus* and from those of other genera of fungus-growing ants cultured at the same time under identical conditions. A scanty, irregular mycelium of unusually fine hyphae grew slowly over the nutrient agar that was unlike the yeast-like *rimosus* fungus, the coarser, bromatial type of Sericomyrmex, Trachymyrmex, Acromyrmex or Atta or the dense cottony Apterostigma fungus.

Transfers were made during the next three months to tubes, flasks and Petri dishes of Sabouraud's dextrose and potato-dextrose agars (both, Difco Laboratories, Detroit, Michigan). Other media were also used later.

Miscellaneous Nutrient Agars

Czapek's agar produced a slight growth of hyphae in three weeks (23°-27° C) that after three additional weeks at similar temperatures became a dense, white mycelium. Malt agar (malt extract-peptone-dextrose) during the above first three weeks produced a luxuriant, typical growth. Trommer's malt extract agar developed a similar growth that in the second month became a mottled brown and white with small white nodules. Steep agar (corn steep liquor) produced a poor growth. Martin's agar with streptomycin sulphate (Soil Sci., 69: 215, 1950) permitted a slow growth.

Other Media

The fungus was grown on 2% agar with a mash of ground rose petals and leaves as the sole source for nutriment and grew normally from October 13 through November until the flask became contaminated in December 1955. December 5 this mycelium was transferred to rose mash agar containing a pine stick, re-transferred on December 13, and by January 3 it had become a denser growth of a bromatial type with the usual thin peripheral mycelium. A later flask of sterilized wet soil and a pine stick of December 5, transferred on December 13 to another flask, had a large, fluffy mycelium extending up on the pine. The surrounding soil being badly contaminated, the stick was placed in another flask on December 27 and, by January 3 the growth was fluffy and extensive.

A pine wood block, 25 mm on a side, on moist sterile soil, following the technique of Dr. T. C. Scheffer and the U. S. Forest Products Laboratory, was covered completely by the fungus between January 25 and May 28, 1956 and was definitely rotted by it. On a similar sweet gum block a dense growth developed that was fed to the ants as described in Part I.

Sterile oats and wheat in flasks produced a dense mycelium, then white nodules from which sporophores resulted, that are described below.

Verification of the Artificial Cultures as True Ant Fungi

The cultures in the potato dextrose agar tubes of June 26-28 grew slowly. On July 25 ants of Colony D were introduced into a June 27 tube of Colony A culture, that now consisted of a thin, dryish and scanty mycelium quite different from fungi from other species of ants being cultured at the same time and under the same conditions. Several ants soon explored the fungus and after an hour most of the ants were clustered on it. On the following morning the ants were found to have deposited one fecal droplet on the fungus and to have cut and scattered small agar blocks. By July 27 the ants had piled agar blocks against a dead ant. The next day the ants were concentrating their attention on the original June 27 inoculum, a piece of substrate covered with fungus, and this fungus was now proliferating a normal ant garden growth of short, dense, upright hyphae instead of the sprawling, thin and appressed mycelium in artificial culture at this time. By July 30 the mycelium surrounding the original block of inoculum was being tended by the ants and had assumed an ant-garden method of growth. The next day the fungus was thriving and the dead ant appeared to be covered with the same fungus. It was transferred to a sterile agar tube and 24 hours later the fungus was proliferating but was being overtaken by a bacterial slime; on August 3 the ant fungus appeared to be growing over the slime but this proved a temporary situation and the tube was discarded when the slime was clearly in the ascendency. In the meanwhile the other ants had been successfully cultivating the original cultured fungus until August 8, when long hyphae appeared in a manner that indicated the ants were losing control. They were dead the next day.

Ants of Colony D that had not been able to maintain their own garden on nutrient agar *(q.v.)* were placed in a tube of the cultured fungus of Colony B on August 7. The fungus was in the form of a floccose mycelium. The ants crawled over this, beating the loose hyphae down, and by the next day had clearly adopted it. More than 12 fecal droplets were on the growth. A heavy, apparently bacterial, contamination surrounded the

fungus but stopped short before it. The ants were dead on the 10th. Six days later the ant fungus was still growing normally and the contaminants had not encroached on it.

Subsequently the ants of the various colonies were given cultured fungi, originally from Colonies A and B, and always accepted them. For example, on March 15 the ants of Colony A, their own garden deteriorating markedly, were given a culture on Sabouraud's agar originating December 29. Overnight the ants removed small masses, adding them to the garden, and fed directly on the remainder, as did the white collembolan *Cyphoderus inaequalis* that infested the nest. Colony B was given a mass of the culture, originally from Colony A, that had grown on a pine stick in a malt agar flask from December 27 to January 9. Within 14 minutes six ants and two Collembola passed by or explored it briefly without eating but by the following morning an ant was on the mass, pulling out small portions of the long, tangled mycelium and eating them; a collembolan was also on the fungus. Colony B, given a culture of Colony A fungus on an agar base on June 7, maintained it for the rest of the month.

FIG. 3. Incipient stages on January 11, 1956 of the first sporophores of the fungus of *Cyphomyrmex costatus* to be produced. The tallest sporophore rises 20 mm from its base. A 125-cc flask of sterile oats inoculated November 15, 1955.

THE FIRST SPOROPHORES (FIGS. 3-5)

The mycelium in the normal gardens of *costatus* consists of hyphae of unusual fineness, without the conspicuous terminal dilatations found in the nests of higher genera. No clamp connections have been seen. There had been no indication of the type of fungus it was, whether belonging to the Ascomycetes, Basidiomycetes or other major group.

It was an Erlenmeyer 125-cc flask of sterilized oats, inoculated on November 15, 1955 and kept in a darkened cabinet, that developed the first sporophores of the fungus of *C. costatus*. For a month (21°-25.6° C except temporary minima of 18° on December 11 and 12) it had developed the usual fluffy, gray mycelium characteristic of artificial cultures of this fungus but later in December the oats became coated in places with a denser white form as well, forming white nodules on the surface of the culture. By January 3 (21-25° C except for a few hours at 19° in the interval) there was an increasing accumulation of these in an otherwise extensive but thin mycelium. On the next few days several nodules took an elongated, upright form and resembled standing oat grains of a flat white color, then they started darkening at the apex of each. By January 7 there were four with the apices constricting from the body as grayish caps. They were given Nos. I, II, III and IV and underwent the growth represented in Table I.

TABLE I. Growth of first sporophores of *Cyphomyrmex costatus*, January 1956, in mm

	No. I			No. II			No. III			No. IV		
	Pileus		Total	Pileus		Total	Pileus		Total	Pileus		Total
Date	Ht.	Width	Ht.	Ht.	Width	Ht.	Ht.	Width	Ht.	Ht.	Width	Ht.
Jan. 7	4	..	..	2	..	..	1½	..	..	2	..	..
Jan. 8	5½	..	..	2½	..	..	2	..	..	2½	..	..
Jan. 9	7½	..	..	4	..	..	2½	..	..	2½	..	..
Jan. 10	10	8	20	4	..	..	3	..	..	3	..	..
Jan. 11	11	10	25	5	4½	20	4	4	13	4	4	17
Jan. 12	12	12	26	5	4½	24	5½	5	16	5	5	24
Jan. 13	13	11½	26	5	5	24	11*	6½	23	6	6	30
Jan. 14	13	11½	26	Removed			7	8†	31	6½	6	32
Jan. 15	13	11½	26				7	8†	33	6	5	32
Jan. 16	12½	11	26				7	8†	32	6	5½	33
Jan. 17	12	10½	26				6	8†	31‡	6	5	31‡
Jan. 18	12	10½	25				Removed			Removed		
Jan. 19	No growth											

*As pressed against the glass.
†Expanding at rim.
‡Strongly curved stipe.

Sections of No. II were made with the assistance of Dr. Raper on January 13 and revealed no spores or basidia but a distinct hymenial layer of the pileus. There was an early indication of gills in the form of short ridges on the underside

of the pileus. The largest free ends of the hymenial layer were about the same diameter as the largest hyphae in a fungus garden (4-6 μ). The outer part of the stipe facing the hymenium was reddish brown in color as was the outer layer of the pileus and both had longer and freer hyphae than in the hymenium but of about the same diameters. No. III and IV were removed on January 17 and sections of No. III made for slides. Sections of both were used for inoculating Sabouraud's dextrose agar Petri dishes. No. III and IV had ridges as in No. I, foreshadowing the gills.

From January 16 no further growth of No. I took place and it gradually darkened and degenerated. By January 18, however, a new cluster of incipient sporophores started development on the opposite side of the flask. There were about 15 nodules in a rosette, each about two millimeters high, elongating and attaining a reclinate to upright position. Also on this date gill sections of the pileus of No. IV, that had been placed on the agar the day before, were proliferating a dense white growth of hyphae, the temperature in the interval of 25 hours being 23-26° C.

This second series developed rapidly and on the following day were darkening at the apices where the pileus would form. They grew into the interior of the flasks where measurements could not readily be made. By January 21 there were 11 with lead-gray pileus clearly differentiated and of about 2-3 mm height as in the first series; four others were smaller and grayish buff. The following day one was clearly out-stripping the others in rate of growth. On the 24th this had a total height of about 23 mm. A third series consisting of two had arisen against the glass 20 mm from the bottom in the mass of oats, each about 13 mm tall and below the first series, but these failed to grow further. On the 25th the longest sporophore was fully 50 mm long and 3-4 mm in diameter and one had expanded its pileus to a spread of 7 mm. The underside was clearly white and with radiate lamellae.

On January 26 two of the second series of sporophores were pushing up against the cotton plug of the flask and the one, which was most matured the day before, now had the outer margin of the pileus reflexed over the top. During the day another pileus opened out to 26 mm in diameter (Fig. 4). Temperatures since the 3rd had been 21-26° C with the vast majority of hours 24° C.

The two sporophores proved to be mature basidiocarps. Gills were white and the upper surface

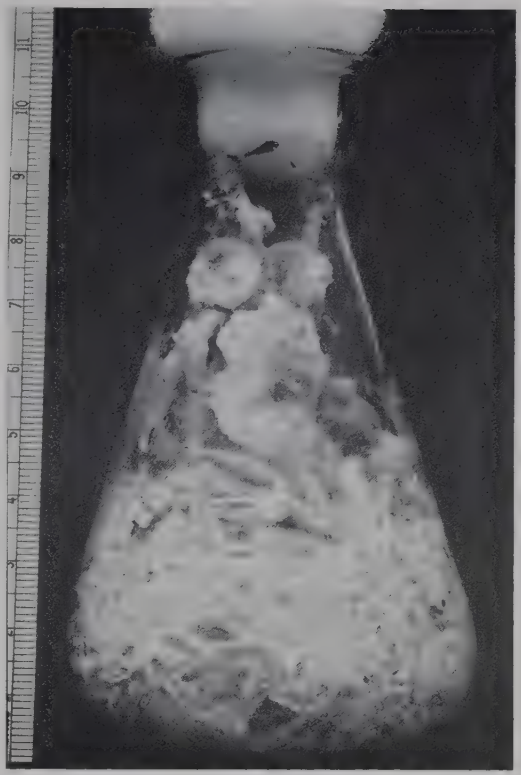

FIG. 4. Mature stage of sporophores in the Fig. 3 flask of the fungus of *Cyphomyrmex costatus*, January 26, 1956. The pileus of the mature sporophore in the center has a maximum diameter as shown of 26 mm.

of the pileus was white except for scales which were grayish brown. These, as shown earlier, consisted of swollen hyphae comparable to those in natural ant gardens but with reddish brown pigment.

Two more sporophores were pushing against the cotton plug the following morning, one being about 60 mm long. The most expanded one had a pileus 27 x 24 mm in maximum diameters (Fig. 5). It and three others were removed, leaving five which were still growing and one which was crushed. One more of the second series was expanding its pileus on January 28 but did not mature on subsequent days, nor did any others, including the remaining one of the first series and the two which started against the glass side in the middle of the substrate layer.

Dr. Alexander H. Smith of the University of Michigan has kindly supplied the description below of the more perfect of the first sporophores to be produced, based on the dried specimen that was sent to him on February 9, 1956.

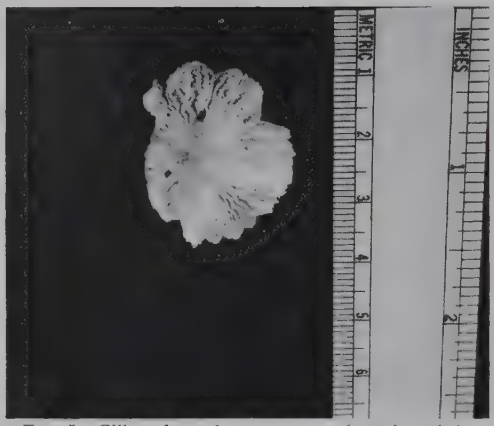

FIG. 5. Gill surface of mature sporophore from below.

"Pileus ± 25 mm broad, with a dark dull brown disc, scaly toward the margin but not conspicuously striate, marginal area white except for scales.

Lamellae free, white, close, drying white.

Stipe 68 mm x 3 ½ mm smooth, annulus movable and dark colored, stipe *drying dark brown.*

Spores 6.5-8 x 4.5-5 μ, elliptic to slightly obovate in face view, subelliptic in side view (with a slight suprahilar-depression), thick-walled, smooth, with an apical germ pore and a small lens-shaped cap over it, hyaline in KOH, *dark reddish brown* in Melzer's; basidia 4-spored, *broadly* clavate, 20-23 x 9-12 μ, sterigmata 3-4 μ long, 0.75 μ at base; pleurocystidia none found; cheilocystidia abundant, 50-80 x 10-15 μ, elliptic-pedicellate with a flexuous apical obtuse out-growth or outgrowth seen as only a short protrusion (all stages present), hyaline, thin-walled, smooth; gill trama hyaline, interwoven; pileus cuticle a loose palisade of clavate-pedicellate cells with fuscous walls in KOH and also the content dark wood brown, many colored filaments also present and ± tangled, content ± wood brown and wall incrusted with a somewhat similarly colored pigment; clamp connections absent."

The flask later produced additional but abortive sporophores. In several instances, from one mass more than one stipe separated while the lead-gray cap represented fused pilei. One of these masses on March 12 showed three well-separated stipes capped by one pileus about 14 x 23 mm in diameter, the mass 20-30 mm high. The pileus was covered by scaling patches of hyphae appearing gray-brown to the naked eye and brown under the microscope. These external hyphae were sub-erect, pigmented and 6-12 μ in diamenter. More internal hyphae of the external layer were paler, 4-12 μ, and with cuticular, pigmented scales. Occasional pigmented hyphal terminations were clavate and to 14 μ in diameter.

Microscopic sections of the gills showed clavate basidia 10 x 30 μ bearing four sterigmata 3-4 μ long. These were stout, curved and pointed and bore elliptical spores 6-8 μ long by 4-5 μ wide. The attached end was pointed. They took the Cotton Blue color in a Lactophenol-Cotton Blue stain.

A 500-cc flask of 2% agar and ground fresh rose petals and leaves, containing a pine stick, was inoculated on December 13, 1955 with a block of agar of 3-4 cc containing a heavy growth of Colony A fungus from an August 1 flask of Sabouraud's agar. By March 23 two long sporophores grew from the side of the agar block, at the base of the pine stick, at angles of 30-40°. One was 75 mm long, with a stipe 2-3 mm thick, and was capped by a conic pileus 5 x 6 mm. The other was 50 mm long. By the next day the latter had fully expanded its pileus to a diameter of 19 x 22 mm. This had 44 gills originating from the center and about 12 additional and shorter gills that were more peripheral. The stipe had grown to 68 mm in 24 hours at 23-25.6° C.

During this period and through June, 1956 abortive sporophores were produced in wheat flasks. Commonly the upper central area of the cultures developed a fluffy mycelium that appeared gray to the naked eye. This consisted of reddish brown hyphae when viewed microscopically. More peripherally at the sides of the shrunken media a dense white growth of hyphae containing white nodules developed. On nutrient agars, as they dried, the mycelium became a mottled grayish brown and white from irregular nodular masses of these colors.

THE SPOROPHORE OF COLONY B FUNGUS

Cultures of Colony B fungus had been identical with those of Colony A during the months of development on similar media under similar conditions.

It was a 150-cc cotton-plugged wheat flask inoculated on January 11, 1956 that produced the first mature sporophore, on May 31. Like the other culture flasks, it had been kept in a darkened cabinet at a temperature of 24° ± 1° C for the vast majority of hours, with extremes of 20.6°-29.4° C. briefly attained in the room containing the cabinet. During this period the wheat had dried somewhat and sterile water had been added on April 14 and May 4.

The sporophore, closely similar to those of Colony A, was cramped in the small flask. When

the stipe was straightened it was 66 mm high and with the partially opened pileus 22 mm in maximum diameter. It grew from the side of the somewhat shrunken wheat, welded into a compact mass by the white mycelium, and developed from a small cluster of white nodules. The outer part of the pileus was scaly brownish gray, the gills creamy white. After drying overnight, it was mailed to Dr. Locquin in Paris at the suggestion of Dr. Smith.

During the following month abortive sporophores developed in the flask as in Colony A flasks.

Verification of the Sporophores as True Ant Fungi

A succession of cultures was made from the original inoculum of June 26, 1955 from Colony A fungus. The ants of the same colony and of the other colonies accepted these artificial cultures, whether raised on Sabouraud's, potato dextrose, wood blocks or other media. It was, therefore, clear that the November 15 flask contained the true ant fungus. From this flask, sub-cultures were made in December that were treated as ant fungi by the ants and had the same characteristics under the microscope. After the sporophores started to develop on January 9, oats from this flask were used to inoculate wheat flasks that developed the mycelial characteristics of all previous pure cultures and this was true of the culture on wheat resulting from an oat of the flask taken January 22.

The stipe of a mature sporophore removed on January 26 was sectioned, and freshly cut pieces were given directly to the four colonies of *C. costatus,* including that from which the original artificial culture was taken in June (see Part I). The ants of these soon explored the fragments, as did the common white Collembola living as commensals in the nest. Within the hour two ants of Colony C were feeding deeply and intently on the juices. The consistency of the stipe was dense and fibrous, quite different from the fungus of the garden. By the following morning ants of three of the other colonies were in attendance and feeding on the stipe fragments. In one it had been shredded as though they had done much feeding and there were Collembola feeding on one side. In Colony C the fragment was in the midst of contaminated substrate and a mite had tunnelled into it. Hyphae were starting to proliferate, the temperature in the 17-hour interval having been 23-26° C.

Fragments of the stipe were given on January 27 to other ants as follows, the results being examined under the binocular microscope in all but one case:

1. A colony of *Atta sexdens.* The ants immediately came up to the piece when it was introduced and explored with their antennal tips without showing hostility. Within a minute a large worker tasted it and 12 minutes later two ants dragged it to one side, where other ants "felt" of it with their antennae and tasted it repeatedly. The following day about ⅓ had been removed and the remainder was discarded.

2. A colony of *Atta colombica.* These ants also explored it as above and tasted it. Six minutes later it was dragged down a hole in the midst of a cluster of ants showing excitement by their antennal and body movements; it was not seen thereafter.

3. A colony of *Acromyrmex octospinosus.* Several ants found it quickly, explored it as above and six minutes later one was cutting it. Within the hour others cut large pieces off it and were tasting them repeatedly.

4. A colony of *Trachymyrmex zeteki.* An ant soon explored and licked it and within ten minutes, under the binocular microscope two ants could be seen to taste it repeatedly, then three licked the entire surface intently. An ant was still feeding 12 minutes later but 18 minutes later none was in attendance.

5. A colony of *Trachymyrmex cornetzi.* Two ants immediately seized the fragment when it was introduced, then an ant approached, only to recoil immediately. One of the first ants cut into it briefly and tasted it at several other sites. An ant was cutting into the large piece 17 minutes later, then carried it about rapidly over the entire feeding chamber for more than 20 minutes as though it were confused. The following day it was discarded but pieces had been removed first.

6. The one ant remaining alive of *Trachymyrmex urichi* that at the time had no fungus of any kind. By January 30 the fragment had proliferated long, fine hyphae but was apparently not manipulated in any way.

7. *Apterostigma mayri* and *A. angulatum:* parts of colonies with a common chamber for foraging. The ants ignored it, as was anticipated, since their fungus is very different.

The behavior of five of the above eight species of other genera indicated strongly that the fungus was close in qualities to their own fungi, for otherwise they would have reacted differently, either by attacking it, by quickly removing it to a discard pile, or at least by not tasting it.

In the meanwhile, the four colonies of *Cyphomyrmex costatus,* each with a flourishing garden of its own, largely ignored the fragments after eating fractions of them. They were, however, eaten by Collembola and mites in these nests.

During February 17 to 23rd a series of abortive sporophores developed in the flask, with the pilei fused together. The stipe of one of these was removed and sectioned for feeding on the 23rd to *Atta sexdens* (two colonies), *A. cephalotes, A. colombica* and *Acromyrmex octospinosus.* The ants of one of the *A. sexdens* colonies and Collembola in the nest fed on the stipe sections for half an hour or more; in the second nest the ants carried it about intermittently, without feeding, for the same period. The ants of *A. cephalotes* clustered about the stipe section, cut out many pieces and ate steadily on the fragments. A large media worker fed intently on the white center part. The *A. colombica* ants removed theirs to an invisible part of the nest. The Acromyrmex also accepted the stipe section and the ants soon cut it into pieces. For two minutes an ant was watched under the 18x binocular microscope while it carried a fragment about in the small cells of the garden, exploring its own fungus with antennal apices. Finally it forced the *costatus* fungus into the side of one of the cells, licking it in several places and pushing it into the garden with its fore tarsi. This ant left but was replaced by a smaller ant that licked the fragment for several minutes. In the meanwhile other pieces of the stipe had been placed in two adjoining cells and these, too, were being licked. The ants were cutting fresh green Bauhinia leaves and treating them in the same manner at the same time.

Ants of the above three *Atta* species, the Acromyrmex and *Sericomyrmex ambalis* were placed in containers with *C. costatus* fungus, growing on agar, on several occasions. There were no clear-cut feeding reactions and no cultivation, although the same ants later fed on other ant fungi. When *Atta sexdens* ants were given access to artificially cultivated fungi of both *C. costatus* and of *Trachymyrmex morgani,* they placed debris and agar blocks on the former as though it were a refuse pile and fed upon the latter fungus.

The ants of Colony B on March 15 were given the cultured fungus from a Sabouraud's agar plate that had been inoculated on February 23. This fungus had developed from a transfer of a piece of pileus from the sporophore of Colony A. Three minutes later an ant was crawling slowly and haltingly over the growth and a minute later it was plucking the loose hyphae before disappearing from view. By the next morning the culture was clearly accepted. Some had been removed and six workers at one time were on the remainder; feces had been deposited on it. By the 19th the latter growth was no longer the uniform lanose type but had been pulled and manipulated by the ants so that it was more a tufted mycelium as in the normal garden. Thirteen fecal droplets were on it. On May 31 the colony was given a piece of the gill of a sporophore that had appeared during the month in a culture made in Panama from their own garden the previous June. The ants soon explored it briefly and overnight cut and used some, discarding the remainder.

The sub-colonies were given sporophore material on several occasions. The female of Subcolony E on January 30 was given a small piece of the stipe of a Colony A sporophore that had been kept on Sabouraud's agar since the 17th. It had developed short hyphal growths in the interval. The ant dragged it to the side of her garden and within a week had built a garden on top of the stipe section, using fragments from her original garden. Both elements were maintained successfully until February 20, when the experiment was terminated. A similar cultured piece of the stipe was given on the same day to the female of Sub-colony F. She, too, adopted it and placed the remnant of her own garden on it. The stipe garden thrived upon the addition of substrate and by April 30 the stipe base was growing two dense, white tubercles of mycelium, far denser than any normal growths in a *costatus* garden. During May the garden deteriorated and her integument assumed a dusty appearance due to her inability to keep entirely clean by herself.

Sub-colony G, now consisting of one female and one worker, was also given a cultured stipe section on January 30. It was on an agar block and the ants removed not only the section but the proliferating hyphae. They made a flourishing garden out of both elements, discarding the agar to a point 5 mm distant, and this flourished until June.

Sub-colony I, given a stipe section on January 30, soon accepted it and added liquid droplets of their feces. The ants also maintained their original garden.

A cultured stipe section similar to the above sections, and from the same Petri dish culture, served as a control. It was placed in the nest of Sub-colony H on January 30 but, since all ants were dead by February 3, there was no subsequent history of ant intervention or care. This section

proliferated hyphae through February 15 that grew uniformly, while in the other sub-colonies the hyphae grew out from the section in the form of clumps or tufts and more luxuriantly. The explanation must lie in the mechanical manipulation by the ants and their deposition of feces or saliva. By the 20th the hyphae had ceased to grow and most had collapsed within the next four days. In the meanwhile there were four denser sites of proliferation, resembling some aggregates in artificial cultures. These were grow- as dense white columns during the first half of March, when temporary drying of the container caused them to darken and shrink. Upon the addition of water to the soil in the container they revived during April.

By the end of April this container made a striking contrast to those of the other sub-colonies. All of them contained identical soil and were kept under the same conditions, yet they had heavy collembolan infestations while this had none. The others had ants and flourishing gardens which served as abundant sources of food for the pests. This container was equally accessible to the collembolans but evidently did not emit sufficient odor of food to attract them.

Identification of the Fungus

Dr. Smith reported *(in litteris)* that the sporophores belong to "a *Leucoagaricus* in the sense of Singer. A *Lepiota* in the Friesian classification. Using the latter classification I would place your fungus in the general vicinity of *Lepiota cepastipes,* but the characters of the cuticle of the pileus distinguish it from that species. . . . *L. subrachodes* Murrill is close . . . but definitely not your fungus."

At Dr. Smith's suggestion, the specimens were sent to Dr. Marcel Locquin in Paris, the authority on the tropical species *Lepiota.* Dr. Locquin writes *(in litt.)* that he is describing them as a new species of *Lepiota.*

The sporophores differ markedly from those described as *Rhozites gongylophora* by Möller (1893) from the nests of *Acromyrmex disciger* in South Brazil and since reported for an *Atta cephalotes* nest in Surinam by Stahel and Geijskes (1941), *Rhozites* is now considered a synonym of *Pholiota* (Singer, Ann. Myc. **20:** 299, 1922), of the Ochrosporae in Agaricaceae.

It is a matter of considerable interest that the only sporophores clearly associated with fungus-growing ants belong to the Agaricaceae. Of these, the *Lepiota* was reared from artificial culture, the *Pholiota* (= *Rhozites)* were found already developed in nature and have not apparently been raised in cultures. The fungus as grown by *C. costatus* appears similar to that reported by Möller (1893) from *C. auritus* and *C. strigatus* in South Brazil although no fruiting stages were produced by him and he did not apply a name to it.

Summary

Cyphomyrmex costatus Mann, a Central American ant two millimeters long, forms a nest in soil with a single fungus garden that is often about 30 x 20 x 10 mm. The fungus grows in the form of dense, short, fine hyphae lacking the pyriform to spherical terminal dilatations of the fungus of most larger attines. Four colonies and their gardens were used in the present study, from two of which pure cultures of the fungus were obtained in the field. The colonies, collected in June 1955, were maintained for a year in the laboratory. During this period the nests, despite repeated changes of the sand or clay soil, were infested with mites, millipeds, Collembola *(Cyphoderus inaequalis),* nematodes and, in one colony, by two spiders *(Triaeris patellaris)* that preyed on the ants and collembolans. One colony lacked the female early in its history yet males matured in the nest from January to April, indicating egg laying by the workers. Alate females were present in the other nests most or all of the year. Sub-colonies were created by combining a few ants or fragments of gardens from several nests and these new combinations were compatible.

The ants were regularly supplied with cassava granules for substrate for their gardens. When these were dusted with powdered yeast extract they were also acceptable. The history of individual granules, when dyed with neutral red or black dyes, could be followed in the gardens. The ants markedly accelerated the development of the ant fungus on the granules by planting tufts of the fungus on them. In one instance 22 discrete tufts were planted within two hours on one particle. The ants also used caterpillar feces *(Danaus plexippus)* for substrate and planted tufts of the fungus on the dissected particles.

The ants fed directly on sections of sporophores of their fungus and incorporated these into the gardens, cultivating the hyphae that grew from them. Artificial cultures of their fungus grown on nutrient agars, wood blocks and other media were equally acceptable.

They fed to a minor extent on the fungus of *Mycocepurus tardus, Trachymyrmex septentrionalis* and its subspecies *seminole* and of *Acromyrmex octospinosus* but were not seen to eat the

fungus of *Cyphomyrmex rimosus, Apterostigma mayri* or *Atta colombica.*

The first sporophores of the fungus of *Cyphomyrmex costatus* were produced from Colony A fungus in a 125-cc flask of sterile oats inoculated November 15, 1955. Sporophores matured in January and February. Another sporophore, from Colony B fungus, matured on May 31 and was produced in a 150-cc flask of sterile wheat inoculated January 11, 1956.

These sporophores have been identified by Doctors Alexander H. Smith and Marcel Loquin as belonging to the genus *Lepiota* (Leucosporae) of Agaricaceae in the Basidiomycetes. They appear to be the first ant fungus sporophores to be produced in artificial culture and the second to be definitely associated with ants. Möller in 1893 proved that sporophores found growing from *Acromyrmex disciger* nests in southern Brazil were the true ant fungus and named them *Rhozites gongylophora,* now considered a synonym of *Pholiota* (Ochrosporae), also in the Agaricaceae. At the present time these are the only names that can clearly be applied to ant fungi.

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THE FOOD OF THE SALAMANDER LEUROGNATHUS.

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Introduction

Very little is known of the biology of the salamanders of the genus *Leurognathus,* especially from the ecological point of view. Moore (1899) described the only species, *L. marmorata,* and Pope (1924, 1928) and Pope and Hairston (1947) presented some general information about its habitat and distribution. Heretofore, these animals have been considered somewhat of a rarity; however, over the last few years almost two thousand specimens have been captured throughout the known range (Martof 1956). This report is based primarily on an examination of stomach contents. About 200 *Leurognathus* were dissected and nearly all of them contained food.

Methods

Specimens were preserved in the field shortly after capture in order to stop their digestive processes and to facilitate recognition of food items. Food organisms were identified as completely as the material permitted. In some instances, identification to species was possible, but, as might be expected, many identifications were based on fragments of food items and were mainly at the higher taxonomic levels. For example, 1.2 percent of the mayflies were identifiable only to order, 40.2 percent to family, 56.6 percent to genus, and 2.0 percent to species.

Only a few observations on feeding were made in the field because *Leurognathus* inhabits rapidly flowing mountain streams where visibility into the water is generally poor due to its rippled or broken surface. However, at one locality a survey was made of the bottom organisms, these were compared with the food items taken from a series of salamanders collected at the same time. In addition, the stomach contents of a series of *Leurognathus* were compared with those of a series of *Desmognathus quadramaculatus* collected at the

same time and place. Because of the practical difficulties involved, no attempt was made to estimate the volume of the food consumed.

Results

One of the most unexpected observations made in this study was of the many small, irregular rock fragments in the digestive tract of *Leurognathus*. In several specimens these occurred throughout the length of the digestive tract and constituted their entire contents. We wondered how the gut of *Leurognathus* survived the abrasive action of these fragments. Although some of these fragments may have been ingested accidentally, most of them undoubtedly were included in the cases of caddis flies taken as food. Since a large number of food items, including caddis flies and their cases, were whole when taken from the stomachs examined, it was concluded that all food items were swallowed whole.

A summary of the items contained in the stomachs of 150 specimens, ten captured in April and twenty in each month from May through November, is presented in Table I. It is obvious that *Leurognathus* is predominantly insectivorous, in fact, about 98 percent of the stomachs contained insects or their parts. Those which lacked insects were occupied by large food items, a salamander in one instance and a crayfish in the two others. Insects constituted 98.5 percent of the 840 food items recognized; seven crayfish, one snail, two mites, and three salamanders, made up the remainder.

Table I. The food of *Leurognathus* as based on an examination of 150 stomachs

	Food Items		Freq. of Occurrence	
	Number	Percent	Stomachs	Percent
Ephemeroptera	401	47.7	119	79.3
Trichoptera	192	22.9	101	67.3
Diptera	115	13.7	45	30.0
Plecoptera	53	6.3	41	27.3
Coleoptera	39	4.6	24	16.0
Hymenoptera	24	2.9	2	1.3
Decapoda	7	0.8	7	4.7
Caudata	3	0.4	3	2.0
Misc.*	6	0.7	3	2.0
Total	840	100.0		

*1 Odonata, 1 Homoptera, 2 Acarina, 1 Megaloptera and 1 Gastropoda

The food insects were almost exclusively aquatic forms. As might be anticipated, most were in the nymphal or larval stage. However, among the 827 insects there were 45 adults (24 ants, 13 mayflies, and eight beetles) and two pupal caddis flies *(Diplectrona modesta)* still in their cases, but apparently ready to emerge. It is surprising that *Leurognathus* is able to feed on these pupal cases which were firmly attached to rocks. The adult insects, which will be discussed later, were very probably obtained in the aquatic habitat.

Mayfly (Ephemeroptera) nymphs were the most abundant prey; they constituted about one-half of the food items. These organisms are in general fragile: except for the mandibles, they have few heavily chitinized parts. Generic determinations were often difficult since they are dependent on the characteristics of the gills or other delicate parts. Ninety seven percent of the mayflies were classified as Ephemerellidae, Baetidae, and Heptageniidae (listed in order of abundance). The Ephemerellidae, are represented in the southeastern United States by a single genus, *Ephemerella;* it constituted 23 percent of all food items. The Baetidae most frequently encountered were *Baetis* and *Isonychia; Centroptilium, Siphlonurus,* and *Pseudocloeon* were represented by single specimens. In the Heptageniidae, Epeorus and Stenononema were identified. Other mayflies encountered were: five Ephemeridae *(Ephemera),* three Caenidae *(Caenis)* and one Baetiscidae *(Baetisca).* All of these mayflies, with the exceptLeurognathus and might be expected in its diet. *Ephemera,* on the other hand, burrows in the sand and silt of quieter waters and is apparently not readily available to *Leurognathus.* The presence of 13 adult mayflies (ten in one specimen) requires no lengthy explanation; they emerge from the nymphal stage near water, the adults oviposit in the water, and myriads drop into the streams after reproducing.

The second most abundant group of food organisms were caddis fly (Trichoptera) larvae which made up nearly one-quarter of the food items. They were easier to identify than were the mayflies because of the heavily chitinized parts such as the head capsule and the legs. Furthermore, case-dwelling forms remained intact until the case itself was broken apart by the digestive processes. These features probably enabled parts of caddis flies to remain in the stomach longer than did those of mayflies, thus biasing our samples in favor of the caddis flies. Ninety-two percent of the caddis flies belong to the Rhyacophilidae and the Hydropsychidae. The rhyacophilids were represented by two genera having very different habits: *Rhyacophila* is large, does not build a case, and is an important predator of aquatic insects; on the other hand, *Agapetus* is small and builds a relatively large stone case. *Rhyacophila* occurred in only eight stomachs, *Agapetus* in 54.

All the Hydropsychidae encountered are similar in habitat; they are web-spinners and do not build cases except for pupation. In this family, *Hydropsyche* was found in 20 stomachs, *Arctopsyche* in four, *Cheumatopsyche* in two, and *Diplectrona* in two. Five other families of caddis flies appeared in our samples. The Philopotamidae were represented by *Trentonius* and *Dolophilus* four times (two each). The Odontoceridae *(Psilotreta)* and the Goeridae were also found in four stomachs each, Lepidostomatidae *(Lepidostoma)* in two, and the microcaddis, Hydroptilidae, in one.

The abundance of the stone-case-builder, *Agapetus*, was at first surprising; however, its general availability probably outweighs any inconvenience that its heavy stone case might have for *Leurognathus*. *Agapetus* is often found in rather exposed positions whereas caddis flies without cases usually secrete themselves in crevices and under stones.

Fly (Diptera) larvae were the third most abundant group of food organisms. They occurred in almost a third of the stomachs examined and involved about one-eighth of the food items. Because of the small size of many, their numerical rank among the food items over-emphasizes their importance. All but one of the 115 dipterans identified belong to the Simuliidae, Chironomidae (Tendipedidae), and Tipulidae. The Simuliidae *(Simulium)*, so characteristic of fast flowing water, appeared in 11 stomachs. When present, they were usually represented by several individuals; this is in keeping with their gregarious habits. Among the Chironomidae, *Spaniotoma* occurred in 17 stomachs and *Pentaneura*, *Chironomus (Microtendipes)*, *Corynoneura*, and *Tanytarsus*, were found once each. Among the tipulids, the distinctive larvae of *Antocha* appeared in twelve stomachs; seven others contained large specimens unidentifiable to genus. Nine stomachs contained gray masses of tissue that were thought to be the remains of large tipulids, but when characteristic hard parts could not be found, these were not counted. Thus it is possible that large, soft-bodied larvae with greatly reduced skeletal parts may be more important than our data show. The only other dipteran encountered was a single dixid *(Dixa)*.

Stonefly (Plecoptera) nymphs made up only 6.3 percent of the total number of food items and were found in 27.3 percent of the stomachs examined. The relatively large size of many of these nymphs makes them more important in the diet of *Leurognathus* than a numerical account indicates. The Perlidae, in which only *Acroneuria* was identified, were encountered in 30 stomachs, Pteronarcidae *(Pteronarcys)* and Peltoperlidae *(Peltoperla)* in four each, Taeniopterygidae *(Brachyptera)* in two, and Leuctridae *(Leuctra)* in one. It is somewhat surprising that this order of insects, so characteristic of the streams inhabited by *Leurognathus*, was not represented by a larger number of specimens. This is especially noteworthy because their nymphs have habits similar to the mayfly nymphs which were so abundant in the stomachs examined.

Beetle (Coleoptera) larvae and adults were relatively insignificant in both numbers and frequency of occurrence. The Elmidae *(Stenelmis)*, a group in which the adults and larvae are strictly aquatic, were represented by seven larvae and seven adults. Among the other beetles were 13 larval Psephenidae *(Psephenus herricki)*, two larval Gyrinidae, and one adult Curculionidae. While *Psephenus* is often a common component of the fauna of streams inhabited by *Leurognathus*, it is difficult to see how the salamander was able to detach these flattened, tightly adhering larvae from the stones on which they live. The single curculionid, a terrestrial weevil, must have fallen into the stream.

The Hymenoptera were represented by 24 ants. Twenty-three were winged and 22 of these were in the same stomach. In all probability a swarm of flying ants settled in or near the stream and thus became available to *Leurognathus*.

The following orders of insects were represented by single specimens: Odonata *(Boyeria vinosa)* nymph, Megaloptera *(Chauliodes)* larva, and Homoptera (Cicadellidae) adult.

Important among the non-insect food items were crayfish and salamanders. These were the largest food items, moreover they are undoubtedly of high nutritive value. In general, items of this type were encountered only in the larger *Leurognathus*. The seven crayfish found were small or medium sized, the largest being about 50 mm in total body length.

An interesting observation involving a crayfish was made on September 16, 1954, at Buck Creek, Clay County, North Carolina. A stone about a foot square was carefully removed from the stream (eight inches deep) and under it an adult salamander about 115 mm in length was observed lying motionless among the small stones of the stream bed. It apparently was watching a small crayfish, approximately 40 mm in length and ten inches away. When the crayfish approached to within about four inches of the salamander, the

latter quickly moved forward and attempted to grasp the crayfish in its mouth. The crayfish managed to swim back and get away from its predator. However, in backing away, it collided with a stone and quickly changed its direction of travel, now moving somewhat toward the *Leurognathus*. The salamander attacked again and this time succeeded in getting a firm hold near the middle of the crayfish. It then proceeded to swallow the crayfish, head first. In the meantime, the crayfish made no attempt to use its chelipeds on the predator. On several occasions, big crayfish have been observed to drive away large *Leurognathus*, and it is very likely that they in turn devour small *Leurognathus*.

The largest food item was a larval *Leurognathus*, about 70 mm in total length. This is the only instance in which cannibalism was noted. Of the two other salamanders included among the food items, one was a larval *Eurycea bislineata*, about 38 mm in total length, the other, a 50-mm plethodontid, too digested for further identification.

Twelve *Leurognathus* contained bits of vegetable material, mostly tiny twigs and fragments of leaves. Much of this material probably was inadvertently consumed when animal matter was ingested. This is especially true of the filamentous algae found in four specimens. On the other hand, leaf fragments could have been included in the cases of lepidostomatid caddis flies.

Other food items included two mites (Acarina), which may have been parasitic on insect prey, and a small snail (Pleuroceridae). It is not known if the snail shell was occupied when ingested. Three Nematoda encountered in the stomachs can hardly be considered food because they probably were parasitic on the *Leurognathus*.

In order to ascertain if any dietary changes occur from one life history stage to another, food from seven adults, seven subadults, and seven larvae was compared. These specimens were collected in the Coleman River, Rabun County, Georgia, on November 14, 1954. No outstanding differences in kinds and numbers of food organisms are revealed by a comparison of these samples (Table II). As is typical of the Caudata in general (Noble 1931), *Leurognathus* restricts itself to an animal diet during both larval and adult life. The main dietary difference in the various life history stages seemed to be in the size rather than in the type of food consumed. As is apparent, the larvae ate more of the small mayflies and chironomids. The adults fed on larger items but even the largest contained very small food items. Among the small items were larvae of *Stenelemis* and the nymphs of *Ephemerella* (both about 1.5 mm in length). Small food items were often whole when removed from the salamanders' stomachs, verifying that they were swallowed intentionally and that they were not included in the stomachs of larger prey. Further-

TABLE II. A comparison of food items from stomachs of seven adult, seven subadult, and seven larval *Leurognathus*, collected in the Coleman River, Rabun County, Georgia, on November 14, 1954

	Adults		Subadults		Larvae	
	Number of		Number of		Number of	
	Food items	Stomachs	Food items	Stomachs	Food items	Stomachs
Plecoptera (Total)	6	4	2	2	5	3
Peltoperlidae	1	1	..	..	..	..
Perlidae	2	2	2	2	5	3
Taeniopterygidae	3	2				
Ephemeroptera (Total)	14	6	11	7	20	6
Ephemeridae	3	2	2	2	..	..
Ephemerellidae	5	3	7	3	14	5
Baetidae	1	1	1	1	4	3
Heptageniidae	5	4	1	1		
Trichoptera (Total)	15	7	10	4	9	6
Rhyacophilidae	10	6	6	3	5	4
Philopotamidae	..	..	1	1		
Hydropsychidae	5	2	2	2	3	2
Goeridae	..	..	1	1	..	..
Diptera (Total)	1	1	5	1	11	5
Simuliidae	..	..	..	..	1	1
Chironomidae	1	1	5	1	10	5
Coleoptera (Total)	2	2	1	1	2	2
Elmidae	1	1	..	..	2	2
Psephenidae	1	1				

more, such minute food items were taken from the stomachs of large salamanders which contained no other food materials.

The number of food items per stomach varied considerably. For example, 41 items were identified in a specimen taken from the Coleman River in June. Included were 25 *Ephemerella invaria*, four *E. walkeri* group, eight *Agapetus*, two *Epeorus confusus*, one Heptageniidae, and one plethodontid salamander about 50 mm in length. Many of the *Ephemerella* were early instars, less than two mm in total length. The average for all specimens was 5.6 food items per stomach.

The monthly distribution of the food items contained in the 150 specimens is shown in Table III. It is immediately apparent that the chief staples are heavily utilized throughout the year. This is made possible by the fact that some species of mayflies, caddis flies, and stone flies complete their life cycles in a few months, while others require one or two years. Thus, immature forms of these orders are available in any season. Although the samples used in compiling Table III

TABLE III. Seasonal variation in the food of *Leurognathus* as shown by an examination of 150 stomachs. (N = number of food items, % = frequency of occurrence)

	APRIL		MAY		JUNE		JULY		AUGUST		SEPTEMBER		OCTOBER		NOVEMBER	
	Chestatee River Lumpkin Co., Ga.						Reed Cr. Rabun Co., Ga.		Pisgah Cr. Haywood Co., N. C.		Jarrard Cr. Lumpkin Co., Ga.		Coleman R. Rabun Co., Ga.			
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Ephemeroptera	87	100	53	90	53	90	43	85	49	75	53	80	20	40	43	85
Trichoptera	6	50	23	70	40	90	38	85	18	45	16	50	18	60	33	80
Diptera	4	40	24	40	30	60	1	5	3	15	34	45	5	15	14	35
Plecoptera	1	10	10	40	15	55	6	25	3	10	3	15	2	10	13	45
Coleoptera	..	..	3	25	4	20	11	25	..	..	17	50	..	..	4	20
Hymenoptera	..	..	..	..	..	..	..	..	23	10	1	5	..	..	..	..
Megaloptera	1	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Homoptera	..	..	..	..	..	..	..	..	1	5	..	..	..	..	..	..
Odonata	..	..	..	..	..	..	..	..	..	..	1	5	..	..	..	..
Acarina	..	..	1	5	..	..	..	..	..	..	1	5	..	..	..	..
Decapoda	..	..	..	..	..	..	..	..	3	15	3	15	1	5	..	..
Caudata	..	..	..	..	1	5	..	..	..	..	..	..	2	10	..	..
Algae	..	..	..	..	..	5	..	..	..	..	..	20	..	..	..	..
Gastropoda	..	..	..	..	..	..	..	..	1	5	..	..	..	..	..	..
Total	99		114		143		99		101		129		48		107	

were from several localities, these data indicate that *Leurognathus* feeds regularly throughout the spring, summer, and fall. Very likely, they also feed regularly in the winter. This conclusion is based on the fact that early spring and late fall collections contain rather large amounts of food. Furthermore, Hamilton (1932) indicated that at Ithaca, N.Y., several *Eurycea bislineata* examined in January had eaten well, in spite of freezing temperatures and much ice in the streams.

In order to learn if *Leurognathus* selected certain organisms as food or if it fed indiscriminately on those occurring in its habitat, we collected a representative sample of the bottom organisms together with a series of *Leurognathus* from the Coleman River, Rabun County, Georgia, on June 1, 1956. The coarse nature of bottom materials made quantitative sampling impracticable. Individual stones were lifted from the stream and examined closely. An attempt was made to collect all macroorganisms. It was felt that the organisms obtained in this manner were representative of those in the stream. The stomachs of twenty of the salamanders were dissected and their contents, 135 insects, were compared with the 250 insects contained in the stream sample.

Considering only the major taxonomic groups (orders) there is general agreement in the composition of the samples (Table IV). Within these orders, however, there are some interesting disparities. Mayflies were the most abundant group of insects in the stream as well as in the stomachs of the salamanders. They constituted about one-half of the food items and had a similar abundance in the stream. However, *Ephemerella* made up only 42 percent of the mayflies taken from the stream but 88 percent from the stomachs; *Epeorus,* 43 percent from the stream but nine percent from the stomachs; *Stenonema,* eight percent from the stream and none from the stomachs. The best explanation for these differences is provided by field observations of the insects. *Ephemerella* occupied exposed places, such as the upper surfaces of rocks, more than did the other mayflies.

TABLE IV. The relative availability and utilization of insects by *Leurognathus* as shown by a comparison of the contents of 20 stomachs with a representative field sample. All specimens were collected at the same time

	RELATIVE ABUNDANCE (PERCENT)	
	Stream	Stomachs
Ephemeroptera	43	50
Trichoptera	34	43
Plecoptera	13	2
Diptera	8	4
Coleoptera	1	1
Odonata	1	..
Total	100	100

Thus *Ephemerella* is probably more vulnerable to predation by *Leurognathus.*

Like the mayflies, the caddis flies, as a group, show close overall agreement in their relative numbers in the stream and in the stomachs of *Leurognathus.* Comparison of the relative abund-

ance of the various genera, however, again reveals some noteworthy differences. Sixty-seven percent of the caddis flies from the stomachs were the stone-case builder, *Agapetus,* yet only about 35 percent of those collected in the stream belonged to this genus. Another stone-case builder, a goerid, made up seven percent of the caddis flies from the stomachs but was unaccountably absent from the stream collection. The free-living *Trentonius distinctus* made up 50 percent of the caddis flies is the stream sample and only seven percent in the stomachs examined. The net-spinning *Hydropsyche* constituted 25 percent of the stream caddis flies but only five percent of those in the stomachs. These differences might be accounted for, at least in part, by the fact that the stone-case builders live in more exposed places on the stream bottom; then too, they are less secretive and less agile than are the other caddis flies. Moreover, as has been pointed out, the resistance of the stone-case builders to digestion probably made their utilization as food by *Leurognathus* appear to be greater than it actually was.

The discrepancy between the relative numbers of stoneflies found in the stream (13 percent) and in the stomachs (two percent) is surprising in view of the similarities between their habits and those of mayflies.

Desmognathus quadramaculatus has been pointed out by Dunn (1926) as being closely related taxonomically to *Leurognathus.* Then too, Hairston (1949) concluded that the closest ecological associate of *Leurognathus* was *D. quadramaculatus.* In order further to clarify the interrelationships might exist between these two species, we examined the stomachs of 20 specimens of each species, collected at the same place and time: Reed Creek, Rabun County, Georgia, on July 11, 1954. The more terrestrial part of the population of *D. quadramaculatus* was not sampled, only those individuals which occurred in the habitat of *Leurognathus* were examined. Even so, the results obtained reveal a considerable difference in the food habits of these species (Table V).

The *Leurognathus* contained a preponderance of mayflies (45 percent) and caddis flies (37 percent). Aquatic beetles and stone flies made up the remainder of the food. On the other hand, *D. quadramaculatus* fed on a greater variety of organisms. The most abundant group represented were ants (25 percent). Flies (19 percent), caddis flies (19 percent), beetles (16 percent) and mayflies (nine percent) made up the bulk of the remaining items. Also included were: 11 Copepoda, three adult Lepidoptera, two Collembola, two Ostracoda and one each of the following: Orthoptera Homoptera, Odonata, Apterygota, and Diplopoda. The most impressive difference in the diets of these two salamanders is seen in the larger number of terrestrial organisms and winged adults of aquatic insects eaten by *D. quadramaculatus* (Fig. 1). These items constituted 64 percent of the food of *D. quadramaculatus,* but only about ten percent of that of *Leurognathus.* It should further be noted that all of the winged insects (ten adult baetid mayflies) in the sample of *Leurognathus* came from a single salamander. No terrestrial forms were present in the *Leurognathus.* Thus, it can be concluded that competition for food by these two species is not very great. Their food niches overlap slightly but nonetheless are discrete.

TABLE V. A comparison of stomach contents of twenty *Leurognathus marmorata* and twenty *Desmognathus quadramaculatus* collected at same locality and time

		L. marmorata		*D. quadramaculatus*	
		Number of food items	Freq. of occurrence %	Number of food items	Freq. of occurrence %
Plecoptera	nymphs	6	25	1	5
	adults	..	..	1	5
Ephemeroptera	nymphs	36	80	11	30
	adults	10	5	..	..
Trichoptera	larvae	38	85	17	45
	adults	..	..	5	20
Diptera	larvae	1	5	13	50
	adults	..	..	10	30
Coleoptera	aquatic	10	20	..	..
	terrestrial	1	5	19	55
Hymenoptera		..	..	30	40
Misc. insects	terrestrial	..	..	9	35
Caudata		..	..	3	15
Total		102		119	

There was only a slight difference in the numbers of food items in the two species; however, the *D. quadramaculatus* contained a much greater volume of food. This observation suggests either that *D. quadramaculatus* has a greater rate of food intake or that its time of feeding differs from that of *Leurognathus.*

Our data on the food of *D. quadramaculatus* are not in complete agreement with those presented by Hairston (1949). The major dissimilarity is the absence of immature mayflies and caddis flies in his sample. Possibly this may be accounted for by differences in the localities and by the fact

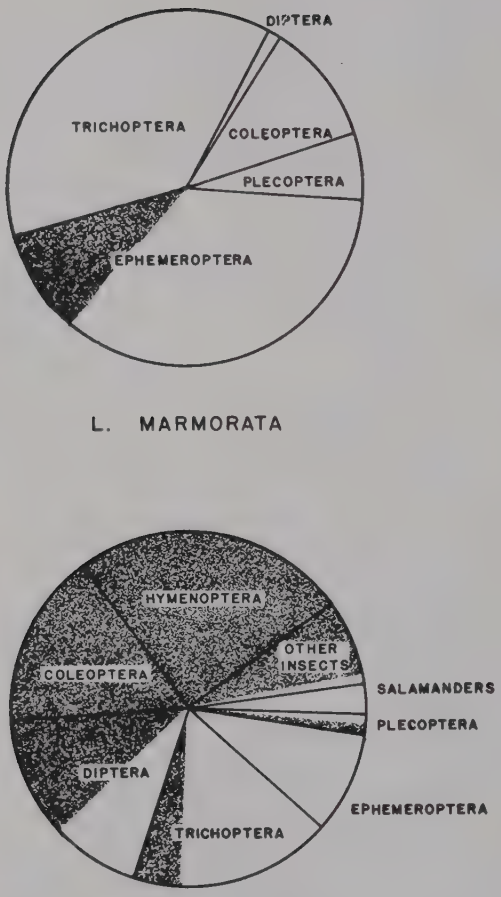

FIG. 1. The relative numbers of food items in the stomachs of *Leurognathus marmorata* and *Desmognathus quadramaculatus*. Terrestrial species and winged adults of aquatic species are indicated by shaded areas.

that our sample was collected primarily from the aquatic habitat.

Actually our data for *D. quadramaculatus* are remarkably similar to those presented by Barbour and Lancaster (1946) for *D. fuscus*. Thus it appears that these two species are ecological equivalents, isolated by topography. The larger *D. quadramaculatus* occupies the montane habitat while *D. fuscus* is primarily an inhabitant of the piedmont and lowlands.

Dunn (1926) noted that *Leurognathus* differs from *D. quadramaculatus* by possessing the following features: skull extremely flattened, internal nares more caudal and farther apart, vomerine teeth absent, and premaxillary fontanelle closed. These anatomical features do not seem to account directly for the differences in their dietary habits.

Discussion

Even though *Leurognathus* appears to feed indiscriminately on a large variety of aquatic insects, it does not eat all insects of reasonable size that are present in its habitat. The high incidence in their diet of active insects, such as *Ephemerella,* supports the conclusion that vision plays a major role in locating food. However, some sort of recognition of prey other than movement is involved. This is important for a current-dwelling species because much nonnutritive material is moved by the passing water. Very likely, size and shape of an object are important in eliciting the feeding reaction. It is possible that the slow moving, yet preferred, *Agapetus* is recognized in such a manner. Furthermore, chemical detection must be involved in locating and ingesting inactive or quiescent organisms, such as *Diplectrona* pupae, and possibly in rejecting others which produce disagreeable stimuli.

Noble (1931) stated that some salamanders (e.g., *Aneides, Cryptobranchus, Ensatina, Pleurodeles* and *Salamandrina)* occasionally eat their own eggs. Presumably, chemoreception is used to identify the eggs as food; accordingly, it is interesting that no evidence of egg eating was observed in *Leurognathus.*

In general, food recognition by *Leurognathus* appears to be similar to that outlined for *Triton* by Matthes (1924). Here the usual order of events is optical stimulation inducing the salamander to approach its prey, followed by chemoreception which evokes the snapping or feeding reaction. However, in contrast to *Triton, Leurognathus* is a current inhabiting form. In such a habitat, the perception of movement alone is not adequate to permit discrimination between animate and inanimate materials. Therefore, some other sensory mechanism, possibly chemoreception, would replace vision, at least in part, in the initiation of the feeding reaction.

Martof (1956) pointed out that the distribution of *Leurognathus* is closely associated with the various drainage systems of the southern Appalachians. Apparently food is not a limiting factor in the distribution of *Leurognathus* because the same or equivalent food items are available in adjacent, uninhabited streams.

Summary

The stomachs of about 200 *Leurognathus marmorata* were examined. This species is predomi-

nately insectivorous. Insects occurred in about 98 percent of the stomachs and constituted 98.5 percent of the 840 food items identified. Forty-eight percent were mayflies, 23 percent caddis flies, 14 percent true flies, six percent stone flies, and five percent beetles. The food insects were almost exclusively the larval or nymphal forms of aquatic species. The chief non-insect food organisms were crayfish and small salamanders. The food organisms varied in size from small mayfly nymphs, larval elmid beetles and chironomid larvae, all of which were about 1.5 mm in length, to a salamander about 70 mm in total length. Regardless of size, food was swallowed whole. Consequently the digestive tracts of many specimens contained impressive amounts of rock fragments, mainly from the cases of ingested caddis flies.

No outstanding dietary changes occurred from one life history stage to another; the major difference observed was that the adult salamanders ate larger organisms. However, the largest specimens contained some of the tiniest food organisms. The major food items are available throughout the year, hence no obvious seasonal change in diet occurred.

A comparison of the insects present in the habitat of *Leurognathus* and those in their stomachs revealed that these salamanders feed on the organisms generally available. However, upon close scrutiny, some important differences in relative abundance and utilization of the insects were disclosed. For example, mayflies of the genus *Ephemerella* were the most common food item; they composed 88 percent of the mayflies in the stomachs but only 42 percent of those in the stream. On the other hand, *Epeorus* and *Stenonema* were moderately abundant in the habitat but were almost excluded from the diet of the salamanders. Among the caddis flies, the stone-case builder, *Agapetus,* was utilized heavily, while the most abundant *Trentonius* and *Hydropsyche* were eaten only sparingly. Compared with their general abundance, the stone flies were not eaten extensively by *Leurognathus.*

An examination of its food organisms indicates that *Leurognathus* feeds somewhat indiscriminately on those animals having the proper movement or size and shape or chemical stimulus, which its sensory apparatus can detect, and that it can overtake and engulf. Thus the diet of *Leurognathus* is determined by the general abundance of bottom organisms and by its ability to detect and capture them.

In contrast to *Leurognathus,* its closest ecological associate, *Desmognathus quadramaculatus,* feeds more heavily on terrestrial organisms and on winged adults of aquatic species, etc. The diet of *D. quadramaculatus* is more similar to the smaller *D. fuscus,* primarily an inhabitant of lower elevations.

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DIFFERENCES IN METABOLIC RATES OF MIGRATORY AND RESIDENT FRESHWATER FORMS OF AN ARCTIC WHITEFISH[1]

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The Eskimo of Barrow, Alaska recognize the whitefish, *Coregonus* (*Leucichthys*) *sardinella* Valenciennes, in freshwater lakes to be generally fatter than the migratory forms found in rivers and the marine to brackish coastal waters. These observations were confirmed: (a) Wohlschlag (1954) noted that the Ikroavik Lake (71°13.5'N., 156°38'W.) forms had greater amounts of abdominally deposited fat than Elson Lagoon (71° 18'N., 156°34'W.) forms and an analysis of weight-on-length regressions revealed that, with increasing lengths, the lake form became disproportionately the heavier and deeper-bodied; (b) Cohen (1954) observed that the two forms had different scale-growth patterns and that the lake forms grew faster; (c) stomachs from fish of both environments were uniformly full, and there were no obvious differences in feeding habits, swimming activities, or environmental temperatures; and (d) while the lake fish tend to remain isolated, the migratory forms enter rivers in the autumn and return to coastal waters in the early summer (Wohlschlag, 1956).

Since it was believed that the differences in body forms of *C. sardinella* from the two diverse environmental types might be due to metabolic differences, an exploratory experimental procedure for field use was devised for the possible detection of any summertime metabolic differences between fish from marine and fresh waters.

It is generally known that a wide variety of animals give the same proportionate metabolic response to temperature and to changes in body weights; excellent summaries of physiological work along these lines have been given by Krogh (1916, 1941), Zeuthen (1947, 1953), and by F. E. J. Fry and coworkers at the Ontario Fisheries Research Laboratory. The adaptive significance of the fact that arctic poikilotherms such as fishes are relatively more active (cold-adapted) at near-freezing temperatures than would be possible for similar species in temperate or tropical habitats has been investigated by Scholander *et al.* (1953). Hoar, Black, and Black (1951) have reviewed in detail the relationships among fish metabolism rates, factors of nervous and endocrine controls, and influences of osmoregulation. There is much information available to indicate that the chief factors influencing metabolism in poikilotherms are body weight, temperature, and activity. Yet there appears to be little known that would supply an incontrovertible explanation of the occurrence and ecological significance of the two forms of *Coregonus sardinella* near Point Barrow.

The experimental field work was made possible with the logistic support of the Arctic Research Laboratory staff whose efforts are gratefully acknowledged. To Mr. Warren C. Freihofer who assisted with the field work special thanks are due. Dr. Norman J. Wilimovsky kindly supplied salinity data for Elson Lagoon waters. The advice and stimulating suggestions by Drs. O. H. Robertson and F. A. Fuhrman of Stanford University have been especially helpful in the organization and interpretation of the experimental results.

EQUIPMENT AND PROCEDURE

A circular, transparent, plexiglass plastic respiration chamber suitable for field use is shown in Figure 1. Approximate dimensions of the chamber are: outside diameter, 45 cm; inside diameter, 25 cm; depth, 10 cm; volume at 10°C, 10,400 ml. Water was added through a funnel-like reservoir and connecting plastic tube; water for oxygen analyses was withdrawn from a plastic outlet tube with pinch clamp; fish were introduced through an eight-centimeter circular cork-sealed lid which could be clamped down when the chamber was in operation. Rotation of the chamber was effected by a large inverted spring-wound phonograph motor from which the chamber was suspended by brass rods. Velocity of rotation was controlled by adjustment of the governor on the motor. Motor and chamber were suspended from a portable derrick rig (Fig. 2) consisting of four three-meter legs. An adjustable pulley system permitted rapid raising and lowering of the motor and chamber which was immersed in water slightly less than one meter deep at the site where fish were captured. Immersion of the chamber assured constant temperatures during a one-hour run.

At the experimental site freshly caught and undamaged fish were placed in the filled chamber, the lid was clamped down, and the reservoir filled.

[1] These studies were aided by a contract between the ONR, Department of the Navy, and the Arctic Institute of North America. Reproduction in whole or in part is permitted for any purpose by the United States Government.

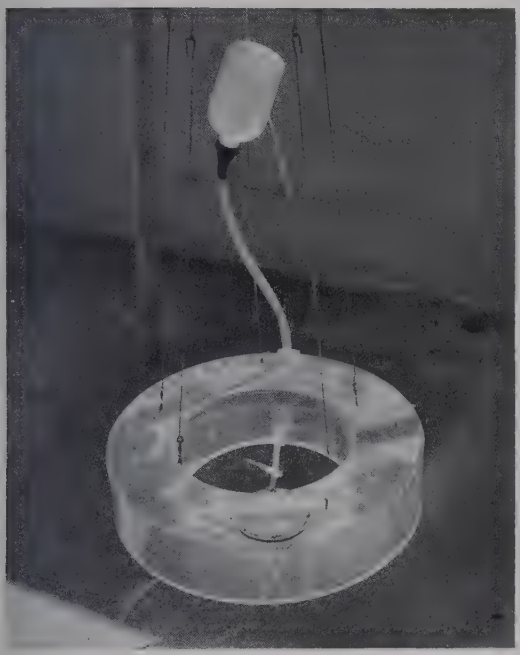

FIG. 1. Photograph showing details of respiration chamber.

FIG. 2. Photograph of complete rig for fish respiration experiments. Inverted motor with respiration chamber shown suspended from apex of derrick by an adjustable pulley system.

As a 265 ml sample was withdrawn for analysis of initial oxygen content, the chamber was simultaneously filled from the reservoir. The chamber was immediately lowered so that it was barely immersed, and it was then rotated at whatever velocity the fish would tend to swim at a more or less constant rate. Each revolution was approximately equivalent to a swimming distance of one meter.

At 10 or 15, 30, 45, and 60 minutes after enclosure of a fish in the chamber, 265 ml samples of water would be withdrawn; each time fresh water from the reservoir would replace the volumes withdrawn. The water-sampling procedure would require one minute or less. The oxygen contents of the samples were determined by the simplified Winkler method as given by Ellis *et al.* (1946). During a typical one-hour run the water temperature would be recorded several times. At the end of a run, weight and other data pertaining to the fish were obtained. Salinity of the Elson Lagoon waters was determined by hydrometer readings which were checked from time to time by chemical analysis.

Oxygen consumption data were obtained for eight *Coregonus sardinella in Elson Lagoon* (71° 22'N., 156°32'W.) near Point Barrow and for fourteen fish of this species in freshwater Ikroavik Lake. An additional series of four *Coregonus* (*Leucichthys*) *autumnalis* (Pallas) was studied at the Elson Lagoon site.

RESULTS AND CALCULATIONS

Field Work

For each of the oxygen content determinations, it was necessary to correct for the addition of fresh water to the chamber and for the volume (weight) displaced by the enclosed fish. In this manner the five (occasionally four) corrected oxygen content values in milligrams for the chamber taken over a period of one hour could be plotted out against elapsed time. The slope of the line through these points was calculated by the least squares method and was the rate of oxygen consumption in milligrams per minute. The rates were converted to milligrams of oxygen consumed per hour for computational convenience; they were essentially linear in all cases. These rates, with the fish weights, chamber rotation velocities, and temperatures, plus derived data are given in

TABLE I. Data for metabolism determinations on *Coregonus sardinella* in Ikroavik Lake and Elson Lagoon and on *Coregonus autumnalis* in Elson Lagoon

Date	Mg O_2 consumed per hr	Log O_2 consumption (Y)	Weight (grams)	Log weight (X_1)	Log mg O_2 consumed per hr per kg (Y_1)	Rotations R. P. M. (X_2)	Temp °C (X_3)	Remarks
Coregonus sardinella, Elson Lagoon:								
31 VII 54.....	38.868	1.590	320	2.505	2.084	0.0	6.7	Sluggish specimen
14 VIII 54.....	24.882	1.396	109	2.037	2.358	12.5	10.8	
16 VIII 54.....	29.292	1.467	143	2.155	2.311	4.5	10.3	
16 VIII 54.....	45.618	1.659	225	2.352	2.307	6.0	10.3	R.P.M. estimated
17 VIII 54.....	35.694	1.553	174	2.241	2.312	6.0	8.9	R.P.M. estimated
17 VIII 54.....	38.976	1.591	188	2.274	2.317	3.5	8.9	
17 VIII 54.....	33.498	1.525	143	2.155	2.370	0.0	9.4	
17 VIII 54.....	31.524	1.499	104	2.017	2.482	5.0	9.4	
Averages:.....	34.7940	1.5350	175.7	2.2170	2.3176	4.69	9.34	
Coregonus sardinella, Ikroavik Lake:								
2 IX 54.....	20.196	1.305	138	2.140	2.165	1.0	9.2	
2 IX 54.....	39.690	1.599	365	2.562	2.036	4.0	9.2	
2 IX 54.....	25.812	1.412	140	2.146	2.266	8.0	10.8	
2 IX 54.....	37.404	1.573	183	2.263	2.310	10.0	10.6	
3 IX 54.....	33.396	1.524	221	2.344	2.179	5.0	9.4	
3 IX 54.....	29.100	1.464	204	2.310	2.154	7.0	9.4	
3 IX 54.....	36.654	1.564	256	2.408	2.156	5.5	9.7	
3 IX 54.....	11.016	1.042	135	2.130	1.912	2.0	9.7	Rough water
3 IX 54.....	20.340	1.308	180	2.255	2.053	5.0	9.4	
4 IX 54.....	41.616	1.619	362	2.559	2.061	5.0	8.3	
4 IX 54.....	27.858	1.445	231	2.364	2.081	3.0	8.9	
4 IX 54.....	30.546	1.485	216	2.335	2.151	2.5	8.9	
4 IX 54.....	16.758	1.224	129	2.111	2.114	7.5	9.2	
4 IX 54.....	25.320	1.403	129	2.111	2.293	7.0	9.2	Repeat run
Averages:.....	28.2647	1.4262	206.4	2.2884	2.1379	5.18	9.42	
Coregonus autumnalis, Elson Lagoon:								
9 IX 54.....	36.852	1.566	157	2.196	2.371	0.0	7.2	
9 IX 54.....	13.494[1]	1.130	124	2.093	2.037	0.0	7.2	Damaged operculum[1]
9 IX 54.....	24.648	1.392	130	2.114	2.278	0.0	6.7	
9 IX 54.....	32.274	1.509	234	2.369	2.140	5.0	7.2	
Averages:.....	31.2580	1.4890	173.7	2.2263	2.2630	1.67	7.03	

[1]Omitted due to injury.

Table I for the *Coregonus sardinella* in Elson Lagoon and Ikroavik Lake and for the *C. autumnalis* in Elson Lagoon. During the period of study, the salinities of Elson Lagoon remained within the narrow range of approximately 23 to 25 parts per thousand.

Oxygen Consumption and Body Weight

Comparisons of the regressions of rate of oxygen consumption on body weight are customarily made on a rectilinear basis with both variables in logarithmic form. The two regressions shown in Figure 3 are fitted by the least squares method and should be construed to apply over the range of temperatures and activities given in Table I.

These two regressions may be compared by the analysis of covariance technique (Table II) to indicate whether the slopes are different and whether there are any differences in the log oxygen consumption rates when these rates are "adjusted" to a common mean log weight. The analysis of covariance procedure is described in many standard statistical texts such as Snedecor (1946) and Goulden (1952). The x_1 and y are differences from the means of the X_1 and Y variables. The data show that both regressions are significantly different from zero but they are not different from each other. However, the test for adjusted means reveals that the two groups consume oxygen at significantly different rates: weight for weight the marine forms consume oxygen at greater rates than do the lake fish.

Oxygen Consumption and Activity

It is useful to extend the foregoing analysis to include the effect of activity on the rate of oxygen consumption. This may be done by comparing the regressions of logarithms of the rates of oxygen consumption per unit body weight (metabolism rates) on the activities (revolutions per minute) for the marine and freshwater *C. sardinella*. An analysis of covariance for the two groups of data is then possible under the assumption that the fish existed within the same tempera-

TABLE II. Analysis of covariance of logarithms of milligrams of oxygen consumed per hour (Y) and logarithms of weight in grams (X_1) for *Coregonus sardinella* in Ikroavik Lake and Elson Lagoon

Location	Degrees of freedom	Sums of Squares and Products			Regression coefficients	Errors of Estimate		
		Σx_1^2	$\Sigma x_1 y$	Σy^2		Sum of squares	Degrees of freedom	Mean square
Lake.....	13	0.30592343	0.24741672	0.34027036	0.8088[1]	0.14017116	12	0.01168143
Lagoon.....	7	0.18508200	0.07326000	0.04720200	0.3958[2]	0.01820389	6	0.00303399
Sum.....	..	.....	.....	.....	.....	0.15837507	18	0.00879861
Average within locations...	20	0.49100543	0.32067672	0.38747236	0.6531	0.17803769	19	0.00937040

The test for adjusted mean log rates of oxygen consumption is F (1, 19 *D.F.*) = 12.47; F is significant since $0.01 > P > 0.001$.

Source of variation:			
Total	0.29485599	20	.....
Average within locations	0.17803769	19	0.00937040
Between adjusted means	0.11681830	1	0.11681830

The test for differences in slope of regressions is F (1, 18 *D.F.*) = 2.23; F is not significant since $0.20 > P > 0.10$.

Source of variation:			
Deviations from average regression within locations	0.17803769	19	.....
Deviations from individual location regressions	0.15837507	18	0.00879861
Difference between location regressions	0.01966262	1	0.01966262

[1] $t = 0.8088/\sqrt{0.01168143/0.30592343} = 4.14$ (12 *D.F.*); $P<0.01$.
[2] $t = 0.3958/\sqrt{0.00303399/0.18508200} = 3.09$ (6 *D.F.*); $0.05> P >0.01$.

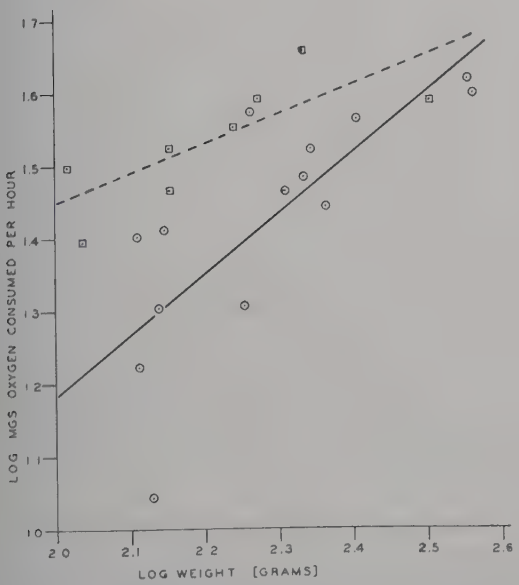

FIG. 3. Logarithmic plots of oxygen consumption rates and body weights of marine forms (squares and broken line) and freshwater forms (circles and solid line) of *Coregonus sardinella*.

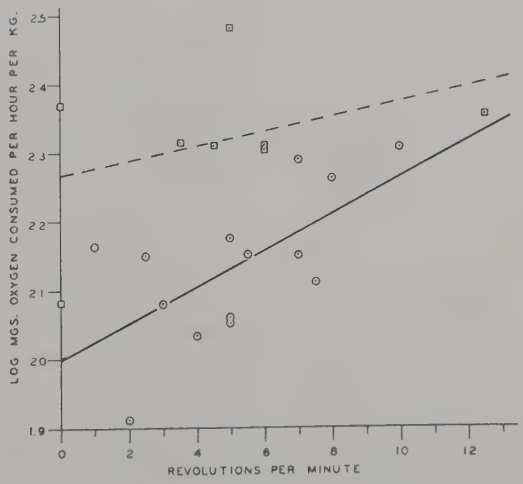

FIG. 4. Relationships between logarithms of the milligrams of oxygen consumed per hour per kilogram of body weight (metabolism rates) and the velocity of swimming for *Coregonus sardinella* in marine Elson Lagoon waters (squares) and in freshwater Ikroavik Lake (circles). One revolution equals about one meter.

ture ranges with the same average temperatures. From Table I it can be seen that this assumption is very nearly correct.

The data may be plotted out as in Figure 4 which shows that the log rates of oxygen consumption per unit body weight (metabolism rates) for the marine fish generally lie somewhat above the rates of the lake fish at corresponding levels of activity. The analysis of covariance data are in Table III where x_2 and y_1 are the differences from the means of the X_2 and Y_1 variables. The data indicate that the regression for the lake fish is

TABLE III. Analysis of covariance of logarithms of milligrams of oxygen consumed per hour per kilogram of body weight (Y_1) and rotations per minute (X_2) in metabolism chamber. *Coregonus sardinella* in Ikroavik Lake and Elson Lagoon

Location	Degrees of freedom	Sums of Squares and Products			Regression coefficients	Errors of Estimate		
		Σx_2^2	$\Sigma x_2 y_1$	Σy_1^2		Sum of squares	Degrees of freedom	Mean square
Lake.....	13	84.30	2.2887	0.151611	0.0271[1]	0.089474	12	0.007456
Lagoon.....	7	109.97	1.1971	0.086162	0.0109[2]	0.073131	6	0.012189
Sum.....	..	.....	.....	.....	.....	0.162605	18	.....
Average within locations...	20	194.27	3.4858	0.237773	0.0179	0.175227	19	0.009222

The test for adjusted mean log oxygen consumption rate per kilogram is F (1, 19 *D.F.*) = 19.49; F is significant since $P < 0.001$.

Source of variation:			
Total	0.354999	20	.....
Average within locations	0.175227	19	0.009222
Between adjusted means	0.179772	1	0.179772

The test for differences in slope of regressions is F (1, 18 *D.F.*) = 1.40; F is not significant since $P > 0.20$.

Source of variation:			
Deviations from average regression within locations	0.175227	19	.....
Deviations from individual location regressions	0.162605	18	0.009034
Difference between location regressions	0.012622	1	0.012622

[1] $t = 0.0271/\sqrt{0.007456/\ 84.30} = 2.880$ (12 *D.F.*); $0.05 > P > 0.01$.
[2] $t = 0.0109/\sqrt{0.012189\ 109.97} = 1.036$ (6 *D.F.*); $0.4 > P > 0.3$.

significantly different from zero while the regression for the marine fish is not and, that these two regressions are not significantly different in slope. When the metabolism rates are adjusted for differences in activities, there is a highly significant difference between them. The marine fish have the higher metabolism rates.

Discussion

Technical Aspects of Field Procedures

In general the apparatus and procedures described above are admirably suited for field experimentation, even under rather difficult arctic conditions. Several precautions must be mentioned however.

Fish much larger than those used in this study would be hampered in their swimming movements in a chamber of the size used. Also larger fish would consume oxygen to the extent that the lowered oxygen tension in the chamber would tend to cause respiration rates to be proportional to the oxygen content of the chamber; the same would be true for smaller fish of the sizes indicated in Table I if they were retained in the chamber for much more than one hour (Krogh 1916). In either case the rate of oxygen decline in the chamber would cease to be constant. For very small fishes, it would be necessary to use several specimens if measurable rates of oxygen consumption were to be obtained with a large chamber as was necessary in the goldfish experiments described by Fry and Hart (1948). The rate of oxygent consumption for several fish might be considerably different from the rate for one fish, other factors remaining the same, due to "social facilitation" (Allee *et al.* 1949).

The technique of making corrections for the additional oxygen introduced in replacing the volumes withdrawn for analyses was necessary since a cumulative error of about five per cent in the total oxygen content of the chamber would occur after one hour. Errors in correction for the volume displaced by the fish and systematic errors associated with the method of oxygen analyses would tend to be the same for each determination of oxygen content in the chamber and would thus be canceled in their effects on the oxygen consumption rate.

One of the greatest difficulties experienced in this study was the determination of the exact rotation velocity of the chamber when irregular movement was caused by wave action. The net effect appeared to result in a lowered metabolism rate. The effect was most noticeable for fish in Elson Lagoon where rough water persisted most of the summer. Even under most adverse conditions, however, a fish would tend either not to swim at all or to swim at a slow but fairly constant rate.

Marine and Freshwater Coregonus

The preceding analyses of covariance show clearly that the slender marine form of *C. sardinella* has a greater respiration rate than does the fatter, deeper-bodied lake form over the range of body weights, temperatures, and activities studied, even though the numbers of specimens studied were small. In a similar fashion an analysis of variance of the log rates of oxygen consumption per unit body weight (metabolism rates) for the two groups of fish yield an F value of 13.83, which, for 1 and 20 degrees of freedom, is significant with a probability slightly greater than 0.001. These comparisons apply to midsummer conditions when both groups are known to have been actively and continuously feeding. It should be noted that the lake forms are extremely fat in comparison to the river or marine forms from time of ice breakup to time of freezing.

The justification for the use of logarithmic oxygen consumption and body weight units has been summarized by Brody (1945). Such data in logarithmic form should yield linear regressions as in the present study. However, logarithmic relationships of oxygen consumption rates to body weights may cease to be linear over a large weight or age range (Zeuthen 1947, 1953) since metabolism rates tend to decline with size. Job (1955) noted that this phenomenon held only for active brook trout. From Table II and Figure 3 the regression of 0.81 for the lake fish is about identical with the standard curves of Krogh and agrees well with the data of Scholander *et al.* (1953) for arctic fishes; the regression 0.40 for the Lagoon fish is undoubtedly low due to the small number of individual measurements.

For a cold water species like brook trout, Fry (1947), Graham (1949), and Job (1955) present data to indicate that the relationships suggested for *C. sardinella* would cease to be linear over a wider range of temperatures; their data also show that temperature and oxygen consumption rates vary differently for fish of different sizes for normally oxygenated water. Fry and Hart (1948), Graham (1949), Gibson and Fry (1954) have indicated that at higher temperatures both activity and oxygen consumption rates tend to decline; Scholander *et al.* (1953) indicated that some inactive fish also tend to consume oxygen at decreasing rates with increasing temperature. It is not known whether such declines would exist for *C. sardinella* near Point Barrow where the natural temperature range would be from around 0°C to about 12°C in marine coastal waters and up to about 14°C in fresh waters. The range of activities (Table I) seems to be rather small for a schooling species, but direct daytime observations in Ikroavik Lake revealed that the fish swam relatively slowly or not at all most of the time and that rapid, darting movements were rare; direct observations on movement were impossible in the turbid marine waters. The data for oxygen consumption rates of *C. sardinella* thus must not be extrapolated too far beyond the range of temperatures or activities met with in this study.

The effect of excitement, injury, and shock can cause large errors in oxygen consumption rates (Graham 1949). In only five of the determinations were the oxygen consumption rates slightly higher during the first few minutes of a one-hour run. Presumably this effect could have been due to handling, but in no case was the over-all hourly rate appreciably affected. The effect of obvious injury is illustrated by the one *C. autumnalis* specimen whose metabolism rate (Y_1) was much lower than the other three uninjured specimens (Table I). One lake specimen studied under very rough water conditions likewise had an unusually low metabolism rate; possibly "motion-sickness" was responsible. Usually the determinations in Elson Lagoon were run in fairly rough water.

Besides the factors of body weight, activity, temperature, and effects of handling, it is generally known that light, temporal rhythms, oxygen tensions, sexual state, age, growth rates, stage of acclimation to existing environment, recency of feeding, social organization patterns, etc. do, in certain cases, influence metabolism rates.

Design and Analysis of Field Experiments

With many possible variables affecting the oxygen consumption rate of fishes and without elaborate laboratory facilities for acclimating experimental fish to carefully controlled environments, serious consideration must be given to field experiments whereby several variables can be handled simultaneously. The possible application of the multivariate analysis technique may be illustrated with the data for the Ikroavik Lake fish. For the data in Table I, an appropriate multiple regression equation is

$$\hat{Y} = a + b_1X_1 + b_2X_2 + b_3X_3$$

where $\hat{Y}$ is the expected log rate of oxygen uptake, a is a constant, b_1 is a partial regression coefficient for the regression of log oxygen uptake rate on weight (X_1) with the activity (X_2) and the temperature (X_3) remaining constant, b_2 is the regression coefficient of log oxygen uptake rate on the activity (X_2) with the variables X_1 and X_3 remaining constant, and b_3 is the regression of log oxygen uptake rate on temperature with the variables X_1 and X_2 remaining constant.

The three partial regression coefficients, the constant a, and measures of statistical variability may be routinely calculated by standard procedures, *e.g.* Snedecor (1946) or Goulden (1952).

For the 14 lake fish the appropriate equation is

$$\hat{Y} = -0.8687 + 0.8910X_1 + 0.0243X_2 + 0.0138X_3.$$

The first two coefficients are highly significant; the third is not, due largely to the small temperature variation. The over-all correlation among these four variables is $R = 0.8683$, which, for 10 degrees of freedom, is highly significant. This means that about $(1 - R^2)$, or 25 per cent, of the variance of the log oxygen uptake rates is not accounted for by the variables of weight, activity, and temperature. It is believed that the measurements of Table I show about the same order of uncontrolled variability as those given by other workers using laboratory animals. Zeuthen (1947) noted that variation among carefully controlled laboratory metabolism determinations would be of the order of 10 per cent.

While the regression for the eight lagoon fish is based on too few degrees of freedom to be more than barely statistically significant, it is interesting that the log oxygen uptake regression on activity is not significant, presumably due to the difficulties in measuring the exact rotation velocities of the respiration chamber.

The multiple regression technique also circumvents the expressions of ratios like the rate of oxygen uptake per unit body weight. The variance of such ratios is often statistically complex so that standard analysis-of-variance comparisons are not possible. Several other advantages of the multiple regression technique are that additional variables can easily be included or eliminated from the equations, and the equations for several groups can be compared, regression for regression, by standard analysis of covariance procedures. Should any of the regressions be curvilinear, there are routine methods of handling the data and making comparisons.

Ecological Implications

Coregonus sardinella and related arctic whitefishes regularly occur in the summer in coastal marine areas where they wander about in search of food (period of *nagul* in Russian); these species migrate into fresher waters during the winter period and adults spawn in the rivers; the very young do not wander out to the sea with the regular seaward movement in the spring or early summer (Berg *et al.* 1949; Nikolskii 1954). Walters (1955) emphasizes these autumnal migrations as temperature adaptations under the hypothesis that the wintertime temperatures of the fresh waters could be tolerated while those of the marine waters (below 0°C) could not. The summertime movement of the whitefishes into the coastal waters for feeding would possibly be advantageous, since the food supply in the more restricted river and estuarine regions would undoubtedly be limited if the entire population remained there during the active growing season. *Coregonus sardinella* is reported by Yukheva (1955) as feeding actively all winter in the Tazov Gulf if plankters are available; and the growth pattern of the scales of Elson Lagoon specimens (Cohen 1954) suggests that their growth occurs slowly but regularly over a much larger part of the year than is suggested by the rapid short-seasonal growth pattern of the Ikroavik Lake fish. During the open water season, this species in both environments feeds constantly and very few specimens with less than full stomachs occur; yet the lake fish not only have a linear growth rate slightly greater than that for the Elson Lagoon fish, they also increase in both weight and fat content much more rapidly with age (Wohlschlag 1954).

The failure of the migratory marine forms of *Coregonus sardinella* to accumulate fat as rapidly as the resident lake forms could thus be explained on the basis that energy requirements are higher in the marine waters and that the migratory forms are not so completely adapted as other more truly anadromous or strictly marine species which are generally quite fat in arctic waters.

Energy requirements for osmoregulation in saline waters might be high enough to account for the greater rates of oxygen consumption of the marine *C. sardinella*, but an examination of the literature on the subject of osmoregulation for more temperate and usually nonmigrating species did not yield adequate information to account for all the implications of metabolism rates with respect to fat storage and the temperatures pertaining to adult arctic species. At this point it is appropriate to note that closely related coregonid species in more temperate waters are rather more confined to freshwaters and that in cold waters movement between marine and fresh waters may not involve the same osmoregulatory restrictions as in warmer waters.

More active endocrine regulation of metabolism upon migration from rivers is quite likely for salmonoid fishes (see review of Hoar, Black, and Black 1951). Robertson (1948) has indicated that there is increased thyroid activity in *Salmo gairdneri* prior to migration from streams to lakes. It is also likely that the iodine content of arctic marine waters is much higher than in fresh

waters so that increased thyroid activity in marine waters could result. Robertson and Chaney (1953) have reported this to be true in a comparison of migratory and freshwater *S. gairdnerii*.

That the migratory *C. sardinella* are more euryhaline than the more truly anadromous *C. autumnalis* is suggested by the observation of only *C. sardinella* (which probably winter in the Meade River) moving back and forth into an estuarine region near Point Barrow where the waters are nearly fresh and very cold in the early summer; when the estuary becomes warmer and more saline later in the summer no *C. sardinella* could be observed, and the *C. sardinella* in marine Elson Lagoon waters generally leave by the first of September when considerable numbers of *C. autumnalis* still remain (Wohlschlag 1956). In this area the *C. autumnalis*, in contrast to *C. sardinella*, are very fat; in Siberian coastal waters the same observations have been made (Berg *et al.* 1949). If the limited metabolism data for *C. autumnalis* in Table I are of the proper order and of lower magnitude than the data for marine *C. sardinella*, they would thus strongly suggest that a more complete whitefish adaptation to marine habitats is accompanied by lower metabolism and more fat accumulation.

Movement to and from the river of winter residence and the movement required to maintain themselves in the rather violent currents of Elson Lagoon would involve much more expenditure of energy by the *C. sardinella* of the lagoon than by those of Ikroavik Lake. While direct observations of the lake fish indicate that they move rather sluggishly, indirect observations suggest that the lagoon fish are generally more active. Even so the analyses of the data in Table I show the metabolism rates of the marine form to be higher than for the lake form over the activity range investigated. It should therefore be emphasized that the total seasonal energy expenditure by a migratory *C. sardinella* is probably greater than for a lake resident due to its higher metabolism rate *and* to its greater amount of movement during the period of migration and summer wandering (*nagul*).

The low metabolism rates of the lake fish could possibly be advantageous for the conservation of oxygen when the fish are confined beneath the heavy ice cover of the shallow lakes, but this possibility might be ruled out tentatively, because the metabolism rates would be reduced to minimum levels at the near-freezing winter water temperatures.

Summary

An exploratory field study of Alaskan Arctic *Coregonus sardinella* revealed that migratory forms in marine waters had higher oxygen consumption (respiratory) rates and higher metabolism rates over the body weight, temperature, and activity ranges studied than did the same species isolated in a freshwater lake. These results make possible an explanation of the reason why the lake forms are fatter and deeper-bodied than the migratory forms. The ecological and physiological implications of the study are also discussed from the standpoint of environmental adaptations.

A specially designed apparatus for measurement of oxygen consumption rates of actively swimming fish is described with reference to field experimentation.

The problem of handling several variables simultaneously was also explored; and it was concluded that multivariate analysis of field data was both feasible and desirable.

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COACTIONS IN LABORATORY POPULATIONS OF TWO SPECIES OF *DAPHNIA*

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The simple mathematical formulations of Volterra (1926) and Lotka (1932), and a substantial body of evidence concerning the effects of interspecific competition on experimentally regulated populations, have strengthened the impression among ecologists that existing patterns of distribution are, in part and perhaps largely, governed by this interaction. Both theory and role of such competition in natural populations have recently been questioned by Andrewartha and Birch (1953, 1954). Although their particular criticism of the competition equations as mathematical models has been answered (Philip 1955), there is no doubt about the limited applicability of the theory in its original form. The most intensive investigation of competition, by Park (1948, 1954) using *Tribolium*, emphasizes that the laboratory model itself presents complexities not inherent in Volterra's theory, which, for example, implies logistic growth for single-species populations. Extinction of one of the two competing species observed invariably resulted, but no a priori prediction as to which one would persist was possible in several of the laboratory environments that were chosen.

More important, the question of the significance of inter-specific competition among animals in natural communities is largely unresolved, nor does the present study bear directly on this point. The type of evidence that exists has been reviewed by Crombie (1947). Direct proof that a species is, in fact, restricted in its prevalence by the presence of competitors is hard to come by. Nevertheless, Elton and Miller (1954), who provide valuable perspective on the problem, feel optimistic about the prospect of gaining meaningful information from community surveys, while maintaining that, at present, the circumstantial nature of the facts, although they are extensive, usually permits alternative explanations.

In an earlier study (Frank 1952) it was observed that members of two genera of Cladocera did not coexist under the experimental conditions provided; in isolation from each other they sustained relatively high densities. The present investigation provides an attempt to apply a similar regime to two species that are more likely to compete in nature. The species *Daphnia magna* and *Daphnia pulicaria* were chosen since they met this requirement and because, unlike most members of their genus, they were relatively easily distinguishable for purposes of census.

The species live in similar habitats, small ponds with high organic content, and have overlapping ranges. Moreover, examination of locality records indicates that they seem not to occur together in one pond. There is, however, a notable scarcity of explicit information on the distribution of Daphnia in small ponds and about the general range of *Daphnia magna*. Thus, as a result of

lack of published species lists, it was possible for a European worker to reach the erroneous conclusion that *Daphnia magna* does not occur on the American continent (Wagler 1936). Granting that the role of competition in the natural distribution of these species is unknown, it seemed that they were highly suitable for a preliminary investigation intended not only to provide another laboratory model, but to define differences in population physiology and behavior that could conceivably influence their relative success in natural habitats.

The present study was supported by grants of the University of Missouri Research Council, which supplied constant-temperature equipment and provided some financial aid. It is a pleasure to thank Thomas Park and Marian B. Frank, who read the manuscript and suggested a number of improvements.

Materials and Methods

As in the past, only pure clones of the experimental animals were employed. The stock of *Daphnia pulicaria,* originally from an Illinois pond, was the same as in an earlier study (Frank 1952). *Daphnia magna* were collected in 1952 by Prof. G. E. Hutchinson from a pond near Pasadena, California. The culture methods described in the earlier paper were modified; certain of the techniques used by Slobodkin (1954) in particular proved advantageous. Only the essentials of the methods will be mentioned here, since husbandry of the animals has been significantly improved. More detailed description of present conditions of culture will be presented elsewhere.

All animals in the main set of tests were subjected to a routine of census and simultaneous removal to fresh medium at 72 hour intervals. This period, rather than the shorter one of previous experiments, was adopted because it proved better for *Daphnia magna,* which tended to die, apparently from clogging of the filtering appendages, when the medium was changed more often. Animals were cultured in charcoal-filtered tap water, to which was added either (a) 1.2 mg per cc of commercial baker's yeast, or (b) 1.8 million cells per cc of *Chlamydomonas moewusi* Gerloff from pure cultures 15-31 days old. Yeast and algae were estimated photometrically after an initial calibration by weighing or haemocytometer count. The following six types of populations were observed for 69 days:

a. In yeast	
D. pulicaria	8 replicates
D. magna	8 replicates
Both species	14 replicates
b. in algae	
D. pulicaria	8 replicates
D. magna	8 replicates
Both species	14 replicates

All populations were started with two animals, aged 10-12 days, per species, and were maintained in baby-food jars 4.5 cm in diameter containing 50 cc of medium. Temperature throughout the experimental period was held at 20° C. Cultures were kept in constant light from 40-watt fluorescent fixtures 24 cm above the water surface. Since not all replicates were begun on the same date, it is possible to check on effects of fluctuations in supposedly constant factors. No obvious correlations between time and populational events were noted.

Before census, animals were separated into two size categories by first passing them through a screen of No. 00 bolting cloth, and then visually separating the few animals that clearly did not fit into the groups so established. Census involved complete count of all live animals, ephippia, and parthenogenetic eggs shed prematurely from the mother's brood pouch. Repeated tests showed that both ephippia and such dropped eggs were inviable. Sex ratios were determined at 15-day intervals in single-species replicates. In mixed populations, sex ratios in *Daphnia magna* were observed at every census after Day 30. Immediately prior to census and change of medium, oxygen tension was estimated with a dropping mercury electrode.

Aside from this main set of tests, mass populations in battery jars containing 8 liters of water were observed somewhat more casually. Two replicates of each of the single species and of the mixed species were maintained in constant light and at relatively constant temperature for a period of 18 months. All cultures were fed a mixture of yeast and algae at weekly intervals. No attempt was made to regulate the amount of food except on a visual basis. The water was not changed during the course of the test, but distilled water was added periodically to keep volume constant. It proved impossible to sample the populations quantitatively. In mixed species replicates, the ratio of the two organisms was estimated monthly by dipping out 600 cc of medium after first stirring the contents of the jar vigorously, but in irregular fashion. If the sample so obtained did not yield at least 100 animals, another was drawn. Because of differential behavior of the two species and of different age classes, the observed ratios provide only a very gross estimate of species

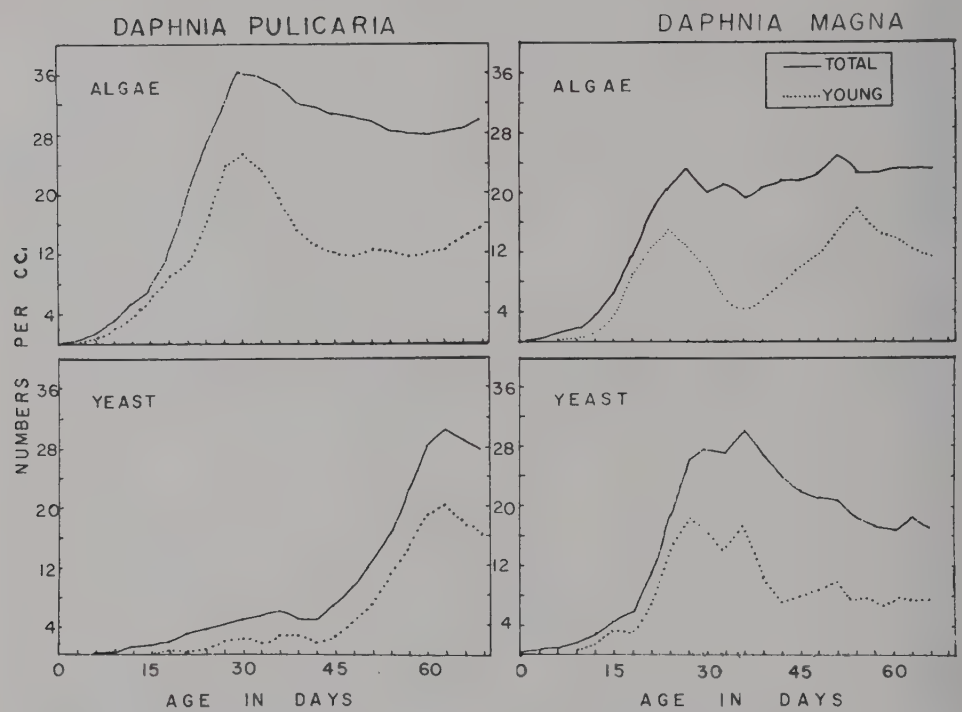

FIG. 1. Average single-species growth form of *Daphnia magna* and *Daphnia pulicaria* in yeast and *Chlamydomonas* cultures.

composition. Contamination of these cultures by other organisms could not be controlled, so that many other interactions besides competition must have existed. Of these complications, availability of bacteria growing in the medium, and growth of epibionts on the Daphnia may certainly have had significant effects.

EXPERIMENTAL RESULT

The single-species control replicates, besides being a necessary adjunct for demonstration of the existence of interspecific competition, are of considerable interest in themselves. They provide a descriptive norm of growth form of the organisms under the selected conditions, and may be subjected to further causal analysis. Figure 1 illustrates average population growth, and presents some crude indication of age distribution. If one limits himself to examination of major trends, it is at once apparent that, as in previous investigations of Daphnia populations (Pratt 1943; Frank 1952; Slobodkin 1954), an initial rise culminates in a distinct peak, followed by a more gradual decrease. Growth form was not observed for a sufficient time to determine whether a second peak would ensue.

Comparison between foods reveals first that the level of population peaks attained by each species shows surprisingly little difference between algae and yeast. This similarity in maximum density is, however, an artifact in the sense that food concentrations were chosen deliberately, from indications of preliminary tests, to equate these points as much as possible. Nevertheless, within species, it appears that algae sustained denser average populations than did yeast. A more striking contrast may be noted in *Daphnia pulicaria,* where rapid population growth commences almost at once in algae, but not until about Day 42 in yeast. The true relations are somewhat obscured by averaging the replicates, as will be seen below.

Comparison between species indicates greater average numbers for *Daphnia pulicaria* than for *Daphnia magna* once the initial growth phase is passed. On the basis of biomass, however, *Daphnia magna,* a larger species, would clearly be superior.

With respect to age distribution the number of young, consisting aproximately of animals from the first to the fourth instar, gives a modified measure of natality similar to that of a moving average. It differs from such a statistic, since some mortality occurs during this age interval, and an increased period of time is occupied by each instar as density increases. With the exception of *Daphnia pulicaria* in yeast, the populations are predominantly composed of young animals during the initial growth phase, or for the first 24 to 36 days. Even in this exceptional case, once rapid growth is established, young animals form about two thirds of the total. After the peak is reached there is a decline in the proportion of young, reflecting greatly decreased birth rate. During this period, many of the adults die and are replaced by recruitment of young (Slobodkin 1954). Unfortunately, determination of death rates did not prove feasible, and the phenomenon can not be fully documented in the present instance. The total effect is a slow decline in numbers, and an increase in average age of individuals. Only in *Daphnia magna* growing in algae was population development sufficiently advanced when the experiments had to be terminated to show good evidence of another cycle of reproductive activity. This difference in behavior of *Daphnia magna* populations in the two types of media suggests a shorter average life span in algae than in yeast. This is supported by the observation at times of census that algal cultures contained a greater amount of debris during this period. Lacking objective data on death rates, it is easy to overstress this point.

The use of averages in describing the experiments is, of course, of limited value, since significant departures from synchrony will be obscured. In Figure 1, moreover, two of the replicates of *Daphnia pulicaria* in yeast were not included in the average; these two cultures became extinct on Days 33 and 57 respectively, without ever having reached a peak comparable to that of other populations. Extinction further emphasizes the precarious condition of this species in yeast, so long as population size is small. Although most cultures eventually grew well, all exhibited a notable initial lag. Total population numbers for alternate replicates of each of the four species and food combinations are graphed in

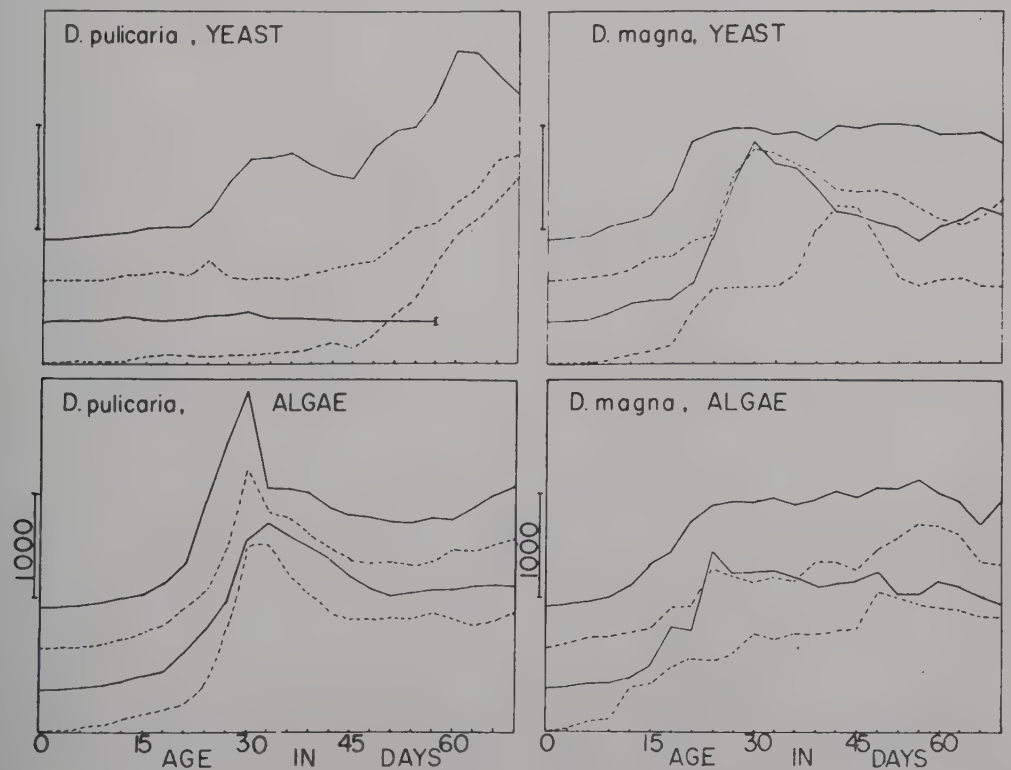

FIG. 2. Growth form of alternate single-species replicates.

Figure 2, in an attempt to give some insight into relative variability. To increase legibility, the vertical scale for successive replicates has been displaced by 400 animals, so that absence of variation would result in parallel families of curves.

By this criterion, *Daphnia pulicaria* in algae grow more consistently than do cultures under other conditions. In yeast, the same species shows great variability. This is stated perhaps in more detail by Table I, which indicates the coefficients of variation at nine-day intervals for each series of replicates. After their extinction, the two previously mentioned *Daphnia pulicaria* cultures are excluded from the calculations. Differences between the species and culture media can be explained only in part. With respect to *Daphnia pulicaria* in algae, culture conditions apparently leave little to be desired, and compare, in terms of variability, with *Tribolium confusum* in a favorable environment (Park 1954). Yeast for these animals clearly is a poor food, at least initially. Those replicates that persisted throughout the experimental period exhibit a variable phase during which populations grew sporadically. Only after approximately one average life span (Frank 1952) were the animals capable of overcoming the deleterious effect of the environment. After densities of about eight Daphnia per cc. were attained, there was no indication that they were still adversely affected. A longer period of observation would have been necessary to discover the permanence of this state. It is likely that yeast causes death selectively of young animals, so that age distribution as well as population density would be significant determinants. Probably bacterial contamination of the yeast is responsible, although perhaps this food organism has itself such an unfavorable influence. No equivalent difficulty is manifested by *Daphnia magna;* they appear to do as well or better in yeast than in algae. In neither medium, however, are their growth curves as congruous as those of *Daphnia pulicaria* in algae.

Certain of the contrasts between species can be established in more detail. Changes in natality are separable into four distinct causes: 1. change in the number of parthenogenetic eggs produced; 2. number of inviable parthenogenetic eggs shed before hatching (referred to hereafter as egg loss); 3. number of adults with ephippial rather than parthenogenetic eggs; 4. number of males in the culture. The number of young animals in populations reflects a compounding of the effects of the first three of these categories. The fourth, however, differs in that mere census yields no estimate of the magnitude of its consequences.

No separate estimate of egg number is available from the present experiments; a marked decrease with density may be expected (Pratt 1943). The other three elements are presented in Figure 3 as percentages of the total adult populations. In both species egg loss occurred as certain times, particularly during early stages of population development. In regard to food, the species behave in opposite ways, *Daphnia magna* having significantly greater loss in algae than in yeast, with the reverse true for *Daphnia pulicaria.* During the active growth period neither species dropped eggs. The number of ephippia, highest in *Daphnia pulicaria* in yeast, increases quite generally as the initial maximum is reached, and declines thereafter. This finding agrees with data from a different species under somewhat similar conditions (Slobodkin 1954). No obvious relation exists between egg loss and production of ephippia.

TABLE I. Coefficients of variation (C.V. per cent) for selected censuses of single species cultures

	DAPHNIA PULICARIA		DAPHNIA MAGNA	
Age in days	Algae	Yeast	Algae	Yeast
9	14.3	37.1	24.6	26.2
18	20.4	59.0	20.7	18.9
27	31.6	55.4	30.7	27.6
36	17.8	140.5	25.9	42.0
45	20.1	185.4	28.8	35.3
54	11.5	81.1	28.2	29.0
63	12.9	55.6	39.4	31.5

The sex ratio strongly suggests a significant species difference that is independent of the type of food. At 30 days, and in the two later censuses for which number of males was observed, *Daphnia magna* cultures averaged 19.6 per cent males, with a range in individual replicates of from 8 to 31 percent. *Daphnia pulicaria* replicates were not found to contain more than 2 per cent males. This difference may perhaps account for the greater variation in development of populations of the former species in contrast to *Daphnia pulicaria* in algae.

To a limited extent it is possible to correlate these events with other variables in the cultures. Measurements of oxygen tensions and egg loss imply some sort of association (Figs. 3, 4). It should be pointed out that since oxygen determinations were made only immediately before census and change of medium, the data do not reflect the entire set of changes that may prove significant. Additional short-term tests show that at moderate densities (to 10 animals per cc) water in the jars attains a minimum oxygen content within four to eight hours after introduction of animals. This low value, usually of the order of

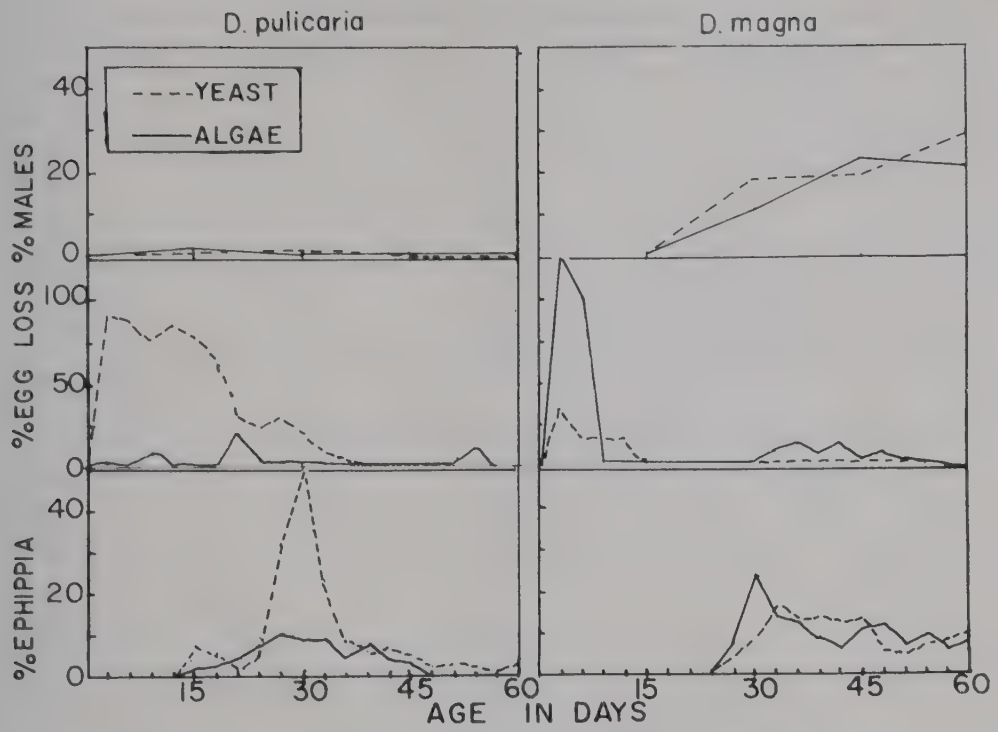

FIG. 3. Average production of males and of ephippia, and egg loss in single-species populations.

0.5 cc of O_2 per liter, is followed by a slow increase. What seems to occur is that at the beginning food contributes a large part of the respiratory loss, not all of which is compensated by entry of air from the surface. As the Daphnia diminish the food supply, less oxygen is consumed by the culture. In algal medium there may be active photosynthesis for a time. This is suggested because it was noted that values of dissolved oxygen increased more quickly and became higher than in yeast cultures. From the data of Figure 4 it may safely be concluded that oxygen lack initially exercises a depressing effect on both species. This could result not only in egg loss, but also in a decline of egg number and of individual growth and feeding rates, as noted by others (Fox, Gilchrist and Phear 1951; Green 1956). However, except when *Daphnia pulicaria* is grown on yeast, such low oxygen concentrations soon rise. During the remainder of the experimental period, food may be assumed to be the major limiting factor.

Ephippia and males show no apparent relation to oxygen concentration, but both seem affected, probably indirectly, by changes in density. It is possible to interpret the present results in the light of a recently proposed hypothesis (von Dehn 1955), according to which lipids in food affect sex determination and sexual egg production, but older theories fit equally well.

In so far as generalization is possible from this limited analytical extension, it seems that the species have similar growth form despite the presence of underlying differences in mechanism of growth limitation. The full significance of such differences cannot be assessed. Its sex composition should presumably confer a decided reproductive advantage to *Daphnia pulicaria,* especially in algal medium. The essentials of single-species behavior were known from preliminary experiments not described here. The present conditions were chosen to demonstrate interspecific competition in the belief that *Daphnia magna* would be favored in yeast, while in algae *Daphnia pulicaria* would be the more successful.

Data from mixed-species replicates, observed concurrently with the cultures just described, are not entirely in accord with this prediction (Fig. 5). In algal medium *Daphnia pulicaria,* as expected, persisted in all 14 replicates, whereas *Daphnia magna* invariably did not. There can be little doubt that extinction was the direct result

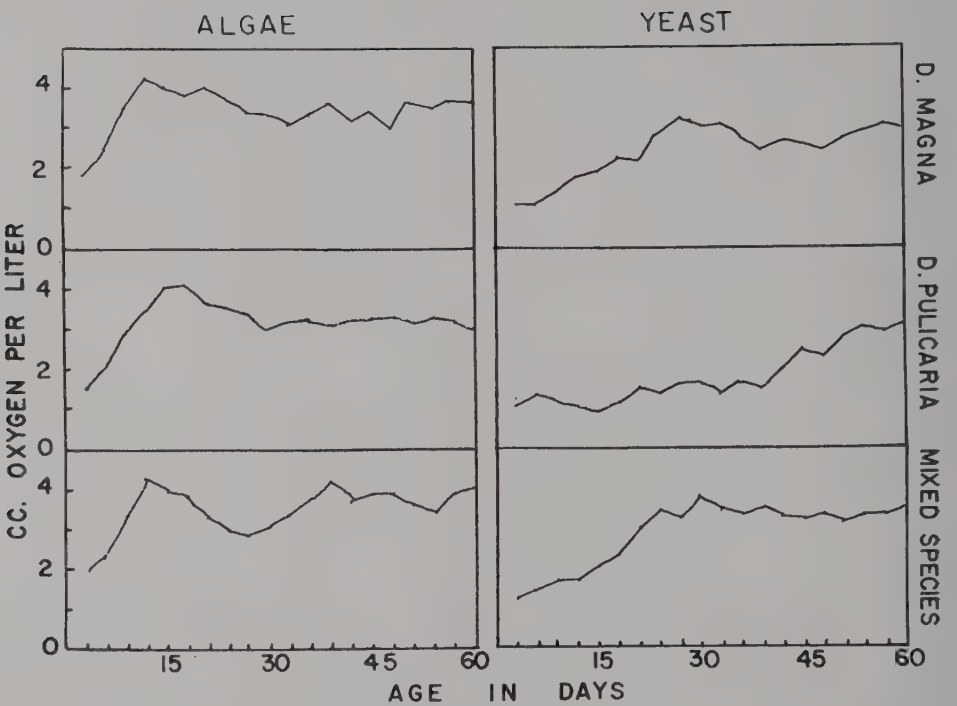

FIG. 4. Dissolved oxygen in single- and mixed-species populations at the end of sucessive census intervals.

of interspecies competition. The analytical data on single species populations suggest the observed outcome: male production, number of ephippia and egg loss all tended to be higher in *Daphnia magna;* moreover, its total population numbers averaged lower than those of the species successful in competition.

In yeast, where *Daphnia magna* might be expected to persist, this result was not realized. During initial stages of population growth, this species does have the faster rate of increase, so that its numbers exceed those of *Daphnia pulicaria.* After Day 27, on the average, *Daphnia magna* starts to decline, and invariably its extinction follows.

More detailed examination shows that, in algae, the populations of the ultimately successful species are inhibited at the outset, when compared to single-species controls. The mean time of occurrence of the population peak is Day 48 rather than Day 30. However, aside from this initial retardation, there seems to be little effect of interspecific competition on *Daphnia pulicaria* here. What causes the major and rapid decline of *Daphnia magna* is not certain, although sex ratio measurements are indicative (Fig. 6). Males predominated during the period of population decline, and formed a greater fraction of the total population than in single-species cultures. In most mixed-species replicates, the last few survivors were entirely males. Since males have, if anything, a shorter life span than do females, it may be conjectured that the immediate cause of extinction is an increase in the proportion of male-determined eggs. Presence of the other species must be assumed as the cause.

In yeast, *Daphnia pulicaria,* far from being inhibited by interspecies competition, increases at a greater rate than in single-species culture. As early as Day 15 its populations in mixed cultures averaged 3.84 per cc as compared with 1.72 for the controls. The difference is significant above the 0.1 per cent level. *Daphnia magna* possibly competes with the other species at this stage, but any such effect is overshadowed by a positive interaction. This, most likely, consists of some sort of detoxification; the simplest explanation is that *Daphnia magna* removes part of the excess food. Thereafter *Daphnia pulicaria* possesses an advantage that may have the same explanation as in mixed-species culture in algae (Fig. 6). Although extinction appears to occur more slowly

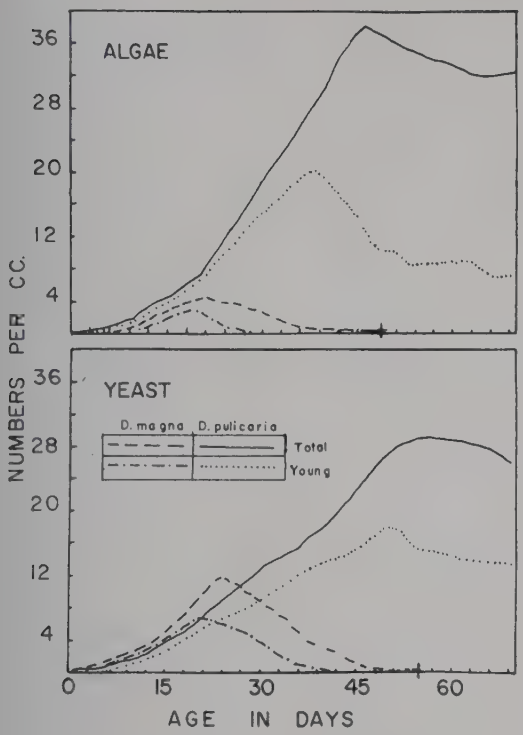

FIG. 5. Average density in mixed-species populations.

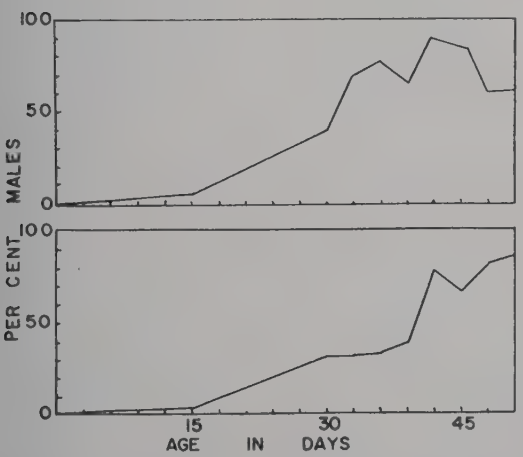

FIG. 6. Percentage of male *Daphnia magna* in mixed-species populations (as per cent of total adult *Daphnia magna*); upper diagram, in yeast; lower diagram, in algae.

in yeast than in algae, the difference is not statistically significant. Time of extinction ranged from Day 33 to 57 in algal medium, with a mean of 45.2 days. In yeast, the first population disappeared on Day 39, the last on Day 66, with an average of 55.3 days.

Information from mass cultures provides a valuable qualifying note to generalization of the foregoing results. This is true despite the facts that sampling of the populations was quite inadequate and that no good estimate of the environmental conditions to which the animals were exposed can be established. However, the major value of these tests is to a considerable extent independent of the demonstration of inter-specific competition as an effective determinant. At least one instructive point emerges whether one considers the difference between single- and mixed-species behavior attributable to such interaction or not. In the jars initially seeded with equal numbers of both species, *Daphnia pulicaria* could not be recovered at the 11th and 18th months respectively (Table II). Single-species populations under otherwise similar conditions persisted well past this period. After *Daphnia pulicaria* had disappeared, the contents of the jars were allowed to dry. Subsequent addition of fresh water caused hatching of ephippial eggs. As neonates were produced, they were removed and counted. After 15 days, when no more ex-ephippial females were observed to emerge, *Daphnia pulicaria* surpassed *Daphnia magna* in hatch by a ratio of 2.3 : 1 and 8.6 : 1 in the two replicates. Certainly, under natural conditions, an apparent result of coexistence of the two species might not be permanent, nor would it necessarily reveal long term trends. *Daphnia pulicaria,* at an apparent disadvantage when the short-range results are examined, may nevertheless be favored if environmental fluctuation, in this case drying, enters as an additional component of competition.

TABLE II. Per cent *Daphnia pulicaria* in samples from mixed-species mass cultures

Month	0	1	2	3	4	5	6	7	8	9
Replicate 1.....	50.0	39.5	55.6	60.6	18.4	15.2	1.7	0.9	1.8	0.3
Replicate 2.....	50.0	46.2	58.8	43.1	46.7	21.0	56.3	32.4	26.4	18.5

Month	10	11	12	13	14	15	16	17	18
Replicate 1.....	0.2	...	...	...	...	...	...	..	.
Replicate 2.....	12.2	3.4	1.0	2.1	1.3	0.6	0.2	0.4	..

DISCUSSION

If the results of the present study are viewed in terms of their relevance as another experimental model of competition, they demonstrate first that, as in all other such cases for which data have been published, two species forced to live together in a simple environment, in which niche diversification is minimal, do not both persist. The case

of these organisms in yeast medium presents a departure from the usual model. There is added a type of coaction which leads to a result more akin to succession than to interspecific competition *per se*. Since there is evidence that a limiting factor, oxygen, operates at low densities, but declines in significance as populations increase, the result, although it was unexpected, is not altogether surprising. *Daphnia magna,* under these conditions, is a model of what Hutchinson (1951) has termed a fugitive species.

When one attempts to compare the present experiments with those concerning competition between *Daphnia pulicaria* and *Simocephalus vetulus* (Frank 1952), the shorter time span during which the losing species survives in the present set of tests is striking. Unfortunately, the conditions under which the studies were conducted differ in a number of respects: amount of medium, type and quantity of food, and period between feedings all are not comparable. However, there are indications that the mechanisms by which competition produces its main result, extinction, are quite distinct in the two cases. In the earlier investigation, a direct density effect was demonstrated; in the present series it seems likely that the primary influence of competition between the species is to be found in its effect on male production of *Daphnia magna.* It is not necessary to postulate that *Daphnia pulicaria* exercises a different type of interference from that produced by equivalent densities of *Daphnia magna.* Possibly there are periods during population growth of this species when by itself, during which reproduction may be limited almost entirely to males. If this happens, population decline followed by resumed generation of females could be expected to follow. It appears that in mixed culture when the decline of total population occurs, relatively few females of *Daphnia magna* remain, and most of these may be past their reproductive peak.

At the present stage of analysis, there is no reason to belive that effective competition is for anything except food. As emphasized by Slobodkin (1954), direct density effects in Daphnia cannot be demonstrated under most conditions. Thus it may prove possible eventually to equate severity of competition with population structure, amount of food supplied, and filtering rate of the population. If other sources of competition should prove negligible, the model would be relatively simple. Nevertheless, except in end result, it would not correspond to Volterra's mathematical model, nor do other mixed laboratory populations approach the latter more closely. Since extinction through competition has repeatedly been demonstrated, it may be suggested that less restrictive theoretical formulations might be instructive. It is encouraging that the problem has recently been revived at this level in two quite diverse ways (Nicholson 1954; Neyman, Park and Scott, 1956).

Speculations about extension of the present results to natural populations can be entertained only at considerable risk of proving wrong. In laboratory culture food quantity appears to be limiting. Whenever populations are dense, no food remains suspended in the open medium by the end of a census interval. If food also limits natural populations, which seems likely (Brooks 1946), concentration rather than amount would be significant, so that a markedly different situation results. The experimental model has several other highly artificial aspects. Mass culture tests were conducted primarily to indicate the proper context of the other laboratory experiments. In small ponds the final outcome of interspecific competition between Daphnia, if it exists, is related more directly to the number of ephippial eggs produced than to vegetative stages in the population. The latter must bear some relation to this long-term interaction, if only in providing a source of ephippia; but there is no reason to think this relation must be direct. One species could exist at relatively low densities, yet leave more resting eggs than another with greater average numbers. It thus seems possible that two events are superimposed: a short-range effect leading to decreased numbers of active individuals during a single season, but perhaps rarely if ever causing apparent extinction; and another, lasting over a number of seasons and ultimately determining species composition.

Summary

1. Single- and mixed-species populations of *Daphnia pulicaria* and *Daphnia magna* were observed in the laboratory for a 69-day period.

2. When alone, both species usually persist in each of two food media, although *Daphnia pulicaria* is severely inhibited by one of these in the beginning.

3. In mixed species cultures that were fed on algae, *Daphnia pulicaria* consistently persisted and may be presumed to cause the observed extinction of the other species. The result could have been predicted from study of the isolated species.

4. With yeast as food, *Daphnia pulicaria* increased more rapidly in mixed- than in single-species replicates, and again caused the extinction of *Daphnia magna.*

5. The presence of two limiting factors, oxygen

and food, at different stages of population history can account for the observed results.

6. The major competitive effect causing extinction of *Daphnia magna* in both foods appears to be increased male production of this species.

7. Mass-culture experiments emphasize that in competition between natural populations of these species, numbers of ephippia rather than of active individuals may be more significant.

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WINTER BURNING IN CENTRAL OKLAHOMA GRASSLAND

Different portions of the Grassland Formation have been subjected to burning either by accidental or purposeful fires. Many workers have reported on the various effects of fires on the grassland (Aldous 1934; Daniel *et al.*, 1943; Hopkins *et al.*, 1948; Penfound and Kelting 1950). The present paper presents data on the effects of fire on the vegetation and certain environmental factors of a pasture plot in central Oklahoma.

Study Area

The study area is a pasture plot that is located approximately eight miles southwest of Norman, along State Highway 9 in McClain County, Oklahoma. Early in February 1952, a grass fire jumped a fire guard and burned a portion of the pasture that had been protected from grazing since July 1949. The fire was brought under control before the entire plot was burned. This presented an excellent opportunity for such a study as mentioned above. Previous studies in this area had shown that four dominant grasses comprised most of the vegetation of the pasture: *Andropogon scoparius, A. Gerardi, Sorghastrum nutans,* and *Panicum virgatum.*[1]

Measurements

The following climatic and edaphic factors were measured: air temperature (weekly maximum-minimum and continuous record), soil temperature (continuous record), precipitation, soil moisture, volume weight of soil, soil reaction (pH), and soil organic carbon (Walkley and Black values as outlined in Piper, 1944).

Weekly determinations of living areal cover also were made. At the termination of the project, in addition to the determination of living areal cover for the various species, the quadrats were clipped at ground level and the oven-dry weight of each of the major species was determined in the individual quadrats.

Environmental Factors

Most of the environmental factors that were measured apparently were unaffected by the fire during the time of measurement (Table I). Volume weight measurements were slightly higher in the control plot than in the burned area during one period but the difference was not statistically significant. The per cent organic carbon in the soil was not significantly different in the two plots. The pH measurements showed only slight variations in the two plots. Although slight variations in the weekly precipitation measurements were evident, the total precipitation for the four-month period was essentially the same in the burned area and in the control area. As the season progressed, soil moisture conditions became more unfavorable in the burned area than in the unburned plot (Table II).

When the temperature data obtained from the two plots were compared, the only real differences were noted in the maximum soil temperatures (Fig. 1). The maximum soil temperature in the burned area was consistently higher than in the control area. At times, there was as much as 13 degrees difference between the two. At any given time, other comparable temperature readings were within a few degrees of one another.

[1] Nomenclature of the grasses is according to the 2nd Edition of Hitchcock's "Manual of the Grasses of the United States."

Table I. Volume weight, organic carbon, pH, and precipitation for the two plots

Factor	Date	Burn	Control
Volume Weight*..	3 - 8 - 52	1.3	1.3
	5 - 9 - 52	1.3	1.4
Organic Carbon...	5 - 9 - 52	1.08%	1.05%
pH.....	5 - 9 - 52	6.82	6.85
Precipitation**...	2 - 20 to		
	6 - 24 - 52	14.00 in.	14.09 in.

*Volume weight, organic carbon, and pH values are each based on 10 samples per plot.
**Each value based on the continuous record of two rain gauges.

Table II. Soil moisture for the two plots (with standard errors) expressed as percentages based on oven-dry weight of the soils

Date	Burn	Control
2 - 20 - 52	16.0±0.9	17.2±0.6
4 - 25 - 52	14.5±0.8	17.3±0.6*
5 - 9 - 52	8.2±0.6	11.0±1.6*

*Difference significant at 0.01 level.

Vegetation

The total areal cover of the living material was greater in the control area than in the burned area during the early part of the period of investigation (Fig. 2). It is of interest to note, however, that after the first few weeks, the areal cover of the grasses was higher in the burned plot than in the unburned plot. Although the differences for the individual species were not statistically significant, the total areal cover of grass was greater at each measurement after April 16. It is the opinion of the writer that this is a real difference. Most of the grass cover of both plots was composed of the typical prairie species (Table III).

Data obtained from the oven-dry weights of the major species were compared with areal cover figures (Table III) for these species. Exceptional correlation coefficients were obtained from the comparison of these two sets of figures. Correlation coefficients were computed in the standard manner as outlined by Snedecor 1946.

Discussion

It is apparent from the data presented that burning had little or no effect on most of the environmental factors measured. The higher maximum soil temperatures obtained in the burned area (Fig. 1) were not unexpected. Much of the litter and duff were burned, thus exposing the soil surface. These data compare favorably with those reported by Aldous (1934). However, Aldous also found lower minimum temperatures in burned plots.

The burning presumably was responsible for the increased grass cover after the second week in April (Fig. 2). Higher soil temperatures in the burned area (Fig. 1) may have been the primary cause of the increase.

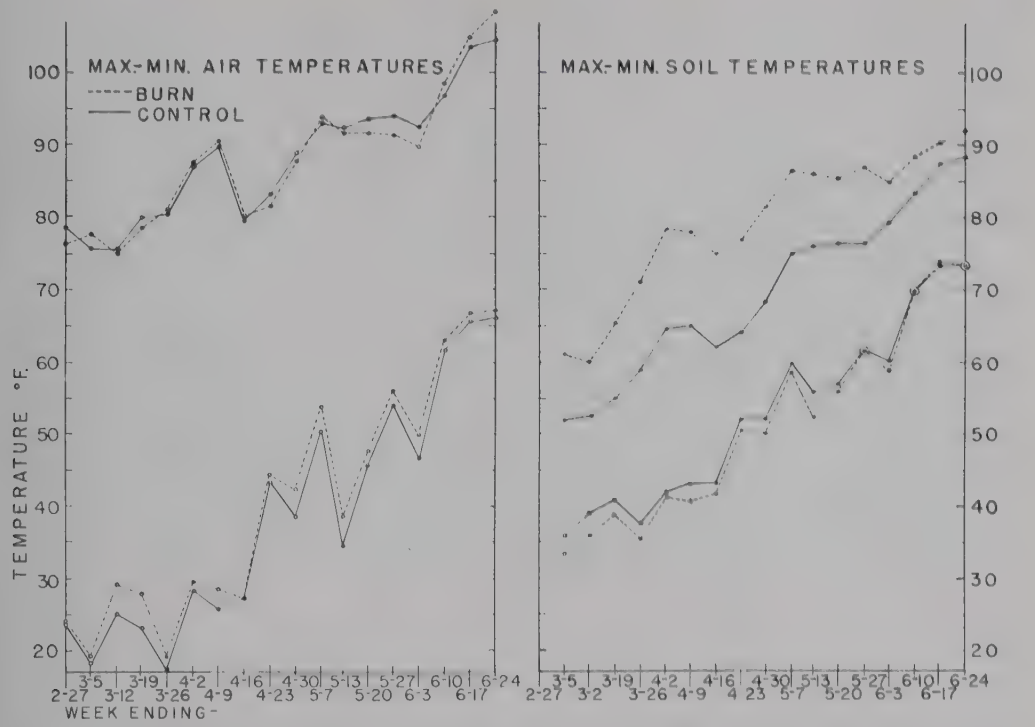
MAX-MIN. AIR TEMPERATURES
BURN
CONTROL
MAX-MIN. SOIL TEMPERATURES
TEMPERATURE °F.
WEEK ENDING
2-27 3-5 3-12 3-19 3-26 4-2 4-9 4-16 4-23 4-30 5-7 5-13 5-20 5-27 6-3 6-10 6-17 6-24

FIG. 1. Weekly maximum-minimum air and soil temperatures from February 2 to June 24, 1952. The air temperatures are averages of five maximum-minimum thermometer readings; the soil temperatures are averages of the readings of two recording thermographs with bulbs buried three inches beneath the soil surface.

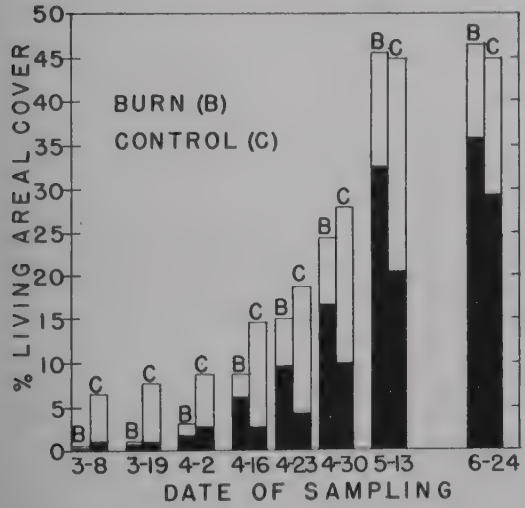

FIG. 2. Seasonal increase in living areal cover. The solid portion of the bar represents grass cover; the clear portion of the bar represents forb cover.

During the early part of the growing season, the areal cover in the control was composed principally of the rosettes of winter annuals. In the burned area, many of these were destroyed. This undoubtedly contributed to the increased rate of growth of the grasses in the burned plot.

TABLE III. Areal cover at the termination of the project (with standard errors)

Species	Areal Cover (%)	
	Burn	Control
Andropogon scoparius	15.9±2.3	11.9±2.5
Sorghastrum nutans	4.7±0.7	3.6±0.8
Panicum virgatum	6.5±1.2	4.0±0.6
Andropogon Gerardi	0.6±0.4	4.3±1.2*
Leptoloma cognatum	3.3±1.0	3.2±0.8
Panicum Scribnerianum	1.4±0.4	0.2±0.1
All grasses	35.9±3.6	29.3±2.6
All forbs	10.5±1.8	15.6±3.1
Total living cover	46.4±3.8	44.9±4.1

*Difference significant at 0.01 level

Apparently the burning had little effect on the areal cover relationships of the various grasses of the two plots. Nevertheless, there was an indication that *Andropogon Gerardi* (big bluestem) was adversely affected by the fire (Table III). The differences in areal cover of this species in the two plots were statistically significant. At the time of sampling, the very low cover percentage of *A. Gerardi* in the burned area was noted. In order to verify these figures, an additional 25 quadrats were studied in

each plot for the sole purpose of checking the amount of this species. In the 25 quadrats of the burned plot, the average cover of this species was less than one per cent; whereas that of the control plot was slightly more than 5 per cent.

TABLE IV. Correlation coefficients, cover versus oven-dry weight, in burned and control plots

Species	Plots	
	Burn	Control
Andropogon scoparius	0.90	0.92
Sorghastrum nutans	0.87	0.91
Panicum virgatum	0.89	0.94
Andropogon Gerardi	....	0.90
All other grasses	0.87	0.79
Total grasses	0.91	0.81
Forbs	0.93	0.97
Total living	0.93	0.88

The correlation coefficients obtained when areal cover was compared to oven-dry weight (Table IV) may prove to be quite significant in grassland investigations. If this relationship could be established as being valid in the grassland areas in general, areal cover could then be used as a good estimate for actual amounts of foliage present. Previous unpublished investigations have indicated that this relationship only holds true during the early part of the growing season. After the inflorescence stalks have elongated on some of the major grasses, there apparently is little or no correlation between the two set of figures. A need for a height factor to be added to the areal cover factor is suggested.

SUMMARY

The effects of fire on various climatic and edaphic factors were measured along with the effects on the vegetation of a tall grass prairie in central Oklahoma.

Burning during the dormant period in late winter apparently had little effect on most environmental factors. Maximum soil temperatures were found to be higher in the burned plot than in the control. As the season progressed, the soil moisture conditions became more unfavorable in the burned plot.

Burning favored the early growth of the various grasses as opposed to the forbs. The only major grass species that was adversely affected by the burning was *Andropogon Gerardi*.

A very good correlation between areal cover and oven-dry weight was found to exist for the individual species of grasses in the two plots.

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EFFECT OF DOMESTIC LIVESTOCK EXCLUSION ON VEGETATION IN THE SONORAN DESERT[1]

INTRODUCTION

This study evaluates the effect of 50 years of protection from livestock grazing on the composition and density of vegetation in a Sonoran Desert area in southern Arizona. The area under study is located west of Tucson, Arizona, within one mile of the present city limits. It is part of the site originally chosen by the Carnegie Institute for the Carnegie Desert Laboratory (MacDougal 1908) Figure 1. Since 1940 the grounds and buildings have been used by the Southwest and Rocky Mountain Forest and Range Experiment Station of the U. S. Forest Service. This change of administration has not affected the management of the grounds which have been continuously protected from domestic livestock grazing since 1906.

The protected area analyzed in this study lies on the west end of the laboratory grounds. The check area lies outside the fence immediately to the west. The area studied slopes gently for the most part from north to south but is divided by numerous small drainages known locally as washes. Before fencing in 1906 the entire region was grazed periodically by domestic livestock; since that time the outside has continued to receive occasional light use. The entire area today is browsed moderately by desert mule deer (*Odocoileus hemionus eremicus*) and javelina (*Pecari tajacu*).

The site is representative of extensive portions of the Sonoran Desert in southern Arizona. Woody perennials dominate the landscape. These are primarily creosote bush (*Larrea tridentata*), foothill palo verde (*Cercidium microphyllum*), ocotillo (*Fouquieria splendens*) and sahuaro cactus (*Carnegia gigantea*). Low growing shrubs such as bur sage (*Franseria deltoidea*), range ratany (*Krameria grayi*) and prickly pear (*Opuntia engelmannii*) as well as several annual and perennial grasses and forbs are also abundant.

Precipitation and evaporation records of the nearby University of Arizona station were consulted as continuous weather records from the Desert Laboratory were not available. The yearly rainfall at the University station averages 10.8 inches; the average yearly evaporation

[1] Arizona Agricultural Experiment Station Technical Paper No. 412.

FIG. 1. A general view of the Desert Laboratory Grounds taken from the U. S. Forest Service laboratory buildings.

rate is 85 inches (Smith 1956). This high precipitation-evaporation ratio has been instrumental in forming the typical shallow grey desert soil of the area and its impervious underlying "caliche" layer of deposited carbonates.

Studies of vegetational changes on the Desert Laboratory grounds after initial fencing and protection of the area in 1906 were carried out by Shreve (1929, 1937). His method, however, mapped and recorded the changes of vegetation in plots inside the protected area only and no controls were provided. While these studies did show changes occurring within the fenced area, they did not indicate whether these same changes might not have been taking place on the outside area also. As excellent photographs of some of his permanent plots are still available, it has been possible to make graphic comparisons of vegetation changes over a fifty-year period (Figs. 2, 3).[2]

STUDY METHODS

The present study compared composition and density of the vegetation both inside and outside the protected area. Sampling was done by Raunkaier's frequency index method as discussed by Gleason (1922, 1925) and Romell (1930). Dice (1948) questioned the validity of the relation between frequency and abundance in a non-randomly distributed vegetation but McGinnies (1934) in a statistical evaluation of this method on similar semi-desert vegetation in Arizona observed a high degree of correlation between frequency and abundance in this vegetation type.

As in McGinnies' study a 1-square-meter quadrat frame was used with a 0.1-square-meter subdivision in one corner. All perennial species were recorded if their basal area fell within the quadrat; annual vegetation was recorded only if it occurred inside the 0.1-square-meter subdivision. The quadrat frames were dropped for a total of 550 samples inside and the same number outside the protected area. Quadrats were spaced in six lines five paces apart with individual quadrats on each line three paces apart, the 0.1-square-meter subdivision always being in the near righthand corner. The results are tabulated in Table I, the significance of the differences encountered being evaluated by the chi-square method under the hypothesis that the counts of a given species would be the same in protected and unprotected areas, using the value of 3.84 (significance at 5% level with one degree of freedom) as the criterion.

Some of the larger plants on the area occurred too infrequently to give adequate data for evaluation by the frequency index method but because of their size they had a dominant influence on vegetation aspect. A comparison was made by count of individuals of these species which were *Cercidium microphyllum, Carnegiea gigantea, Fouquieria splendens, Opuntia engelmannii* and *Ferocatus wislizeni.* All individuals of these species occurring in long, narrow 10-acre plots within each study-area were counted. The final results (Fig. 4), as compared with the results from the frequency index count for these species, showed a significant variation only in the case of *Cercidium microphyllum.* This species was significantly less abundant in the protected area.

DISCUSSION

On both the protected and unprotected areas the same species occurred in approximately the same order of abundance. On the protected area several more species were recorded than on the unprotected area but, because of the low total number of quadrats in which these new species occurred, their presence was not significant. Most of these same species were also noted on the unprotected area but did not occur in sufficient numbers to be recorded inside the quadrats. The most notable change under protection was an over-all increase in density of the vegetation. This was indicated by the lower number of hits where no vegetation was recorded and the in-

[2] The authors are indebted to the Rocky Mountain Forest and Range Experiment Station for making Figure 2 available.

FIG. 2. Plot 16 as it appeared in March 1906.

FIG. 3. Plot 16 photographed in February 1957.

FIGS. 2, 3. Vegetation changes over a period of fifty years on the Carnegie Desert Laboratory grounds.

TABLE I. Results of quadrat analysis in unprotected and protected areas

Name	No. of Hits		% Frequency		Significance of Difference
	Unprotected	Protected	Unprotected	Protected	
Acacia constricta	8	9	1.5	1.6	None
Annuals	332	346	60.3	63.0	None
Aristida spp.	9	13	1.6	2.4	None
Aristida ternipes	...	3	....	.5	None
Ayenia microphylla	12	8	2.2	1.5	None
Bouteloua trifida	2	29	.2	5.3	Increase
Calliandra eriophylla	4	15	.7	2.8	Increase
Carnegiea gigantea	1	1	.2	.2	None
Cercidium microphyllum	7	2	1.1	.4	None
Coldenia canescens	9	22	1.6	4.0	Increase
Condalia spp.	...	1	....	.2	None
Dalea spp.	1	...	.2	....	None
Ditaxis spp.	...	1	....	.2	None
Ferocactus wislizeni	...	1	....	.2	None
Fouquieria splendens	3	13	.5	2.4	Increase
Franseria deltoidea	324	252	58.9	45.8	Decrease
Janusia gracilis	...	2	....	.4	None
Jatropha cardiophylla	4	9	.7	1.6	None
Krameria grayi	93	147	16.9	26.7	Increase
Larrea tridentata	64	73	11.6	13.3	None
Lycium berlandieri	...	2	....	.4	None
Mammillaria microcarpa	...	1	....	.2	None
Menodora scabra	...	2	....	.4	None
Muhlenbergia porteri	3	14	.5	2.6	Increase
Opuntia spp.	6	17	1.1	3.1	Increase
Opuntia engelmannii	19	24	3.5	4.4	None
Pappophorum mucronulatum	...	1	....	.2	None
Parthenium incanum	...	2	....	.4	None
Psilostrophe spp.	5	18	.9	3.3	Increase
Tridens muticus	19	49	3.5	9.0	Increase
Tridens pulchellus	131	210	23.8	38.2	Increase
Zinnia spp.	...	1	....	.2	None
No Vegetation	91	57	16.7	10.4	Decrease

creased frequency of many species on the protected area. It was concluded that the lack of appreciable invasion of new species noted on the unprotected area was probably due to the amount of grazing to which the area has been subjected, a degree of use too light to affect the original vegetation and facilitate the invasion of new species.

A shrub, *Krameria grayi,* palatable to both domestic livestock and game, and three grasses, *Tridens pulchellus, Tridens muticus,* and *Bouteloua trifida,* showed the greatest increase under protection from grazing. This would seem to point to the importance of these plants, even though not occurring in dominant amounts, in the composition of the original undisturbed vegetation of the *Cercidium microphyllum-Franseria deltoidea* habitat.

The density of annual vegetation was not visibly affected by grazing treatment. The study was not made, however, at a time of year conducive to a satisfactory analysis of annuals; severe drought during the two preceding growing seasons also affected this vegetation class. The only observable effect of treatment on *Larrea tridentata* was its less vigorous appearance on the protected site. No effect was noted on *Opuntia engelmannii.* The most significant decrease recorded under protection was noted for *Franseria deltoidea.* This species, although already the most abundant single species and a dominant part of the vegetation on the protected area, has increased perceptibly even though subjected to a disturbing factor such as moderate livestock grazing. There was also an apparent decrease of *Cercidium microphyllum* on the protected area, but this may have been due to the non-random distribution and low density of the species within the limited areas studied.

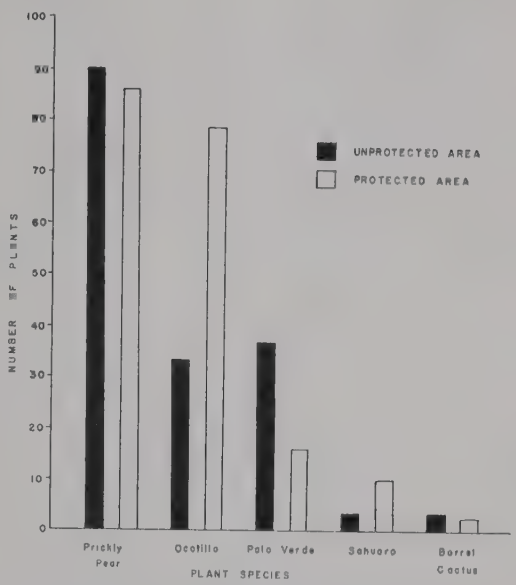

FIG. 4. Results of the count of total individuals of several species in ten-acre plots in both areas.

The photographic comparison presented in Figures 2, 3, and 4 shows the vegetational changes on a plot used by Forrest Shreve in his studies. Many of the changes itemized above can be observed in the photographs. The reduction of *Larrea tridentata* from 1906 to 1956 is quite noticeable as is the increase in density of the grasses and shrubs that have replaced the Larrea. The plot and the surrounding area now have a more diversified plant cover than they had fifty years ago.

SUMMARY

The effect of fifty years protection from livestock grazing was evaluated on an area in the Sonoran Desert using Raunkaier's frequency index method. No appreciable invasion of new species had taken place on the unprotected area and fifty years protection caused no significant change in composition. The most notable change encountered was the over-all increase in plant density on the protected area, with perennial grasses and a palatable shrub, *Krameria grayi,* showing the most significant increases. An exception was *Franseria deltoidea* which was the only dominant species with a significant decrease in density on the protected area. The other dominant species, *Larrea tridentata,* showed no change in density.

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OBSERVATIONS ON THE GROWTH RATE OF THE IMMATURE BERMUDA SPINY LOBSTER, *PANULIRUS ARGUS*[1]

This paper will present some observations made on the growth rate of immature individuals of *Panulirus argus* (Latreille) found in Bermuda. The study is based on work begun in 1951 and was made possible by a grant from the Bermuda Government.

Growth rates or age estimates have been given for *P. argus* in the Caribbean (Smith 1948), Florida (Crawford and De Smidt 1922; Dawson 1949; Dawson and Idyll 1951), the Bahamas (Smith 1951), and Cuba (Martinez 1948); the age estimates given by these authors vary from two to seven years for approximately the same size of animals in different localities.

METHODS

All measurements in this paper refer to carapace length. Where other authors have given data for *P. argus* in inches or in terms of total length, approximate conversions have been made by means of graphs presented by Creaser (1952).

Measurements were made to the nearest millimeter with a millimeter rule. Repetitive determination showed an error of plus or minus one millimeter for lobsters larger than around 80 mm, while specimens smaller than 60 or 70 mm were relatively consistent. Inasmuch as the data for length frequencies are grouped by 10-mm classes, this variable is probably not significant. Most of the animals for moult studies were measured to the nearest tenth of a millimeter with vernier calipers.

The data were obtained from two different sources: (1) from lobsters retained in the laboratory for varying lengths of time exceeding two weeks, and (2) from lobsters recently brought in from the field. In the first group, measurements were taken of the increase in carapace length per moult from lobsters maintained in the laboratory up to several months and which underwent ecdysis two weeks or more after capture. These specimens were kept in large indoor concrete tanks supplied with running seawater and were well fed every two days with chopped fish or minnows; uneaten food was cleaned out the following day to prevent fouling of the water. Part of the data on captive lobsters was kindly put at the writer's disposal by Dr. Dorothy M. Travis, who recently worked in this laboratory on the moulting process of *P. argus* (Travis 1954).

The second source of material consisted of measurements of lobsters caught by trap from the South Shore and Ferry Reach (Fig. 1) and by hand collecting plus traps where the water was very shallow (see Sutcliffe 1952). Some measurements of commercial catches from the Nonsuch area of the South Shore were also utilized for the length-frequency study. Moult increment data on newly caught lobsters were obtained from specimens which underwent ecdysis in less than a week after capture.

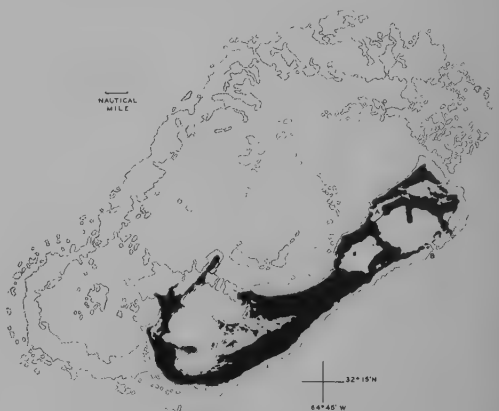

FIG. 1. Sketch map of Bermuda and reefs. The dotted lines represent the three-fathom contour; A, Ferry Reach; B, South Shore.

RESULTS

To determine possible effects of laboratory conditions on growth, moult increments were averaged as in Table I (data partly from Dr. Dorothy M. Travis, personal communication). A statistical comparison was made of the percent increase per moult in the 20-30 mm size class of the recently caught and laboratory maintained animals. The resultant value of t is somewhat greater than that required for significance at the one percent level. Although there is considerable individual variation, it seems clear that animals maintained in the laboratory do not increase as much per moult as those which have already begun the cycle in the field and undergone ecdysis shortly after capture. There was no indication that there was an appreciable difference in growth in the two sexes with the small sizes examined.

It has been shown (Sutcliffe 1952) that the size composition of the populations in Ferry Reach and adjacent

[1] Contribution No. 228 from the Bermuda Biological Station.

TABLE I. Statistical information comparing the percent increase per moult (carapace length) of recently-caught (week or less) and laboratory-maintained (two weeks or more) animals in 20-30 mm size class

	Recently-caught	Laboratory-maintained
No. of individuals	12	19
Mean % increase per moult	14.32	9.49
Standard deviation	4.26	7.74
t	5.01	

areas differs markedly from that of unprotected waters such as the South Shore. Recent investigation indicates that this is typical of Bermuda. There is segregation with respect to size (and thus to age) in the two areas, so these two populations will be treated separately. Figure 2 shows length-frequency compilations at two-month intervals of 1,435 lobsters caught in the two localities. Classes are grouped at 10-mm intervals with percentages in terms of catch in the Reach or on the South Shore. Actual numbers are given in Table II. While the sample is small, the peaks are readily apparent in Fig. 2 and the immature (less than 90 mm) classes increase in size throughout the year, slowly in the winter and faster in the summer. The absence of the 10-mm class in the two periods following August-September is a result of no hand collecting because of bad weather and other factors. It should be pointed out that while the grouping would include all lobsters from 5-14 mm in the 10-mm class, this class actually was composed mostly of 6-8 mm specimens. It may be seen that the 10-mm size class increased to around 20-30 mm by April-May 1952. Thus the 30-mm group found in April-May 1951 must have been in the 10-mm category in the August-September period in 1950, for a careful search in April-May 1951 showed no smaller specimens than those indicated. Following the 30-mm class throughout the period of observation, it would seem to increase to some 70 mm by April-May 1952. Going back again to April-May 1951, this 70-mm group may be followed until it becomes indistinct in August-September when this size class is presumably migrating out and being absorbed by the mature lobster population represented by the dotted line of the South Shore sample. It is significant that the percentages of lobsters less than 94 mm on the South Shore were highest from August to December. It seems reasonable to believe that the 70-80 mm group of April-May achieves sexual maturity (90 mm or more) before the onset of the next breeding season the following March or April. Apparently, then, a period of about three years is required for a lobster to grow from around 6 mm to a size of 90 mm at sexual maturity in Bermuda.

DISCUSSION

According to Mackay and Weymouth (1935), the increase per moult of the Pacific edible crab, *Cancer magister,* was considerably less when the animals were maintained in live wells and aquaria than when under natural conditions. This was particularly true of the smallest sizes, the difference in growth becoming considerably less as the animals got larger. Templeman (1936) found that lobsters (*Homarus americanus*) kept in live cars grew less per moult than those moulting after capture. However, feeding was poor. Marshall (1948) gives data obtained from *Panulirus argus* kept in live cars wherein only three out of ten moulting animals showed an increase

TABLE II. Numbers of lobsters caught in 2 localities (see Fig. 1)

	Ferry Reach	South Shore
Apr. - May 1951	76	84
June - July	156	197
Aug. - Sept.	120	65
Oct. - Nov.	34	62
Dec. - Jan. 1952	39	158
Feb. - Mar.	55	193
Apr. - May	48	148

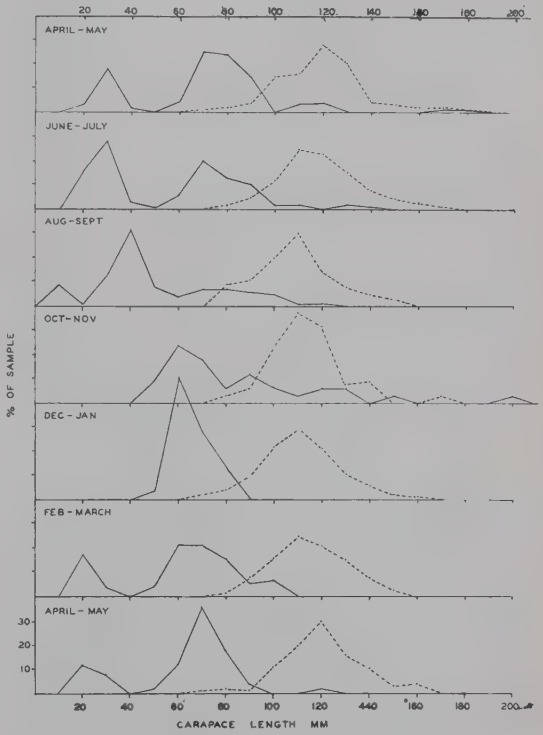

FIG. 2. Length frequencies of 1,435 lobsters by two month intervals in terms of percent of sample from Ferry Reach (————) or South Shore (----------). Absence of 10-mm class in October-January result of no hand-collecting—see text.

in length, five showed no growth, and two a decrease in size. He indicates that this is not necessarily normal for this species. Burkenroad (1951) points out that at least for shrimp, growth of captive specimens cannot be presumed to be applicable to the wild populations. According to Travis (personal communication) growth of laboratory-maintained specimens of *P. argus* improves after a time, possibly as a result of acclimation, although, she points out (Travis 1954), laboratory growth does not duplicate feral conditions. In view of these findings and the results shown in Table II, expectation of obtaining a growth rate from laboratory animals that would be indicative of that occurring under field conditions was abandoned.

Table III summarizes age estimates for *Panulirus argus*

TABLE III. Summary of age estimates (from metamorphosis) and size of female at sexual maturity given by various authors for *P. argus*, *P. japonicus*, and *P. longipes*

Author	Locality	Age estimate for given size: Years	Age estimate for given size: mm	Size of average female at sexual maturity
Panulirus argus				
Smith 1948	Caribbean	6	95	70 - 80
Martinez 1948	Cuba	2 - 3	95 - 140	>70
Smith 1951	Bahamas	7	95	45
Crawford and De Smidt 1922	Florida	....	.....	>76
Dawson 1949	Florida	6	"market size" (>85)	70
Dawson and Idyll 1951	Florida	....	.....	Agree with Smith 1948, 70 - 80
Present report	Bermuda	3	90	90
Panulirus japonicus				
Nakamura 1940	Japan	2	50	40 - 45
Panulirus longipes				
Sheard 1949	Australia	1 - 2	44 - 51	44 - 51 (?)

and two related species. It may be seen that there are decided differences in age estimates of *P. argus* for approximately the same size of lobster. An age of six to seven years for a 95-mm animal in Florida and the Bahamas is compared to an estimate of about three years for a 90-mm specimen in Bermuda. There are no supporting data given with the estimate of Martinez (1948).

Aside from the possibility of two different races of lobsters and considering undoubted growth differences imposed by varied environmental conditions, it is surprising that the Florida populations seem to take so much longer to grow particularly in view of the warmer waters encountered there. It is possible that a discrepancy is involved in that some have based their estimates on the growth of mature individuals. Templeman (1936) has shown that the growth per mount of the female of *Homarus americanus* decreases considerably at maturity, as was found for *Cancer magister* by Mackay and Weymouth (1935). In Bermuda mature females of *P. argus* do not moult for a period of five or six months during the breeding season (Sutcliffe 1952)—a time of year in which the younger stages grow considerably. The mature growth rate cannot be considered indicative of the growth of immature animals.

The comparative length of time from hatching to metamorphosis and to the 6-mm size cannot be considered for the time being. Little is known yet of the larval history in Bermuda. Lewis (1951) indicates that the phyllosome stages may take six months in Florida waters.

Of interest is a consideration of the size of females at sexual maturity and the conditions of temperature in which they are found. In Fig. 3 is shown a graph of the size of females at sexual maturity at Bermuda, Miami, and the Bahamas against the percentage of the year when the water temperature is above 24°C (monthly averages Bermuda-local records, Miami-U. S. Coast & Geodetic Survey 1947, Bahamas—Meteorological Office, Nassau, personal communications). It may be seen that there is apparently an inverse correlation between size at maturity and temperature conditions—larger lobsters in colder waters. In this connection, Travis (1954) has shown that for laboratory animals, at least, there is little

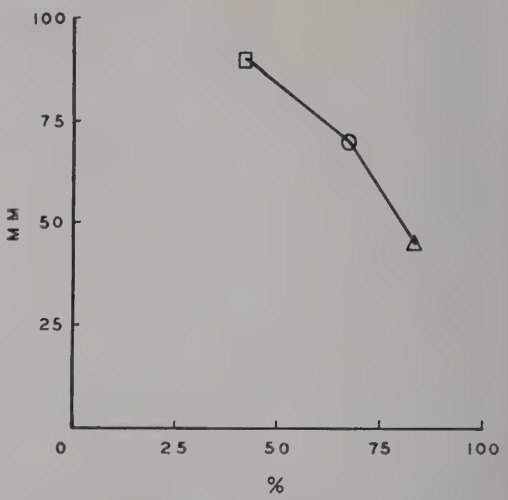

FIG. 3. Ordinate—sizes (carapace length) at sexual maturity of female lobsters (*P. argus*) in three localities: □ Bermuda; O Miami; Δ Bahamas. Abscissa—percentage of the year surface water temperatures fall above 24°C.

significant growth with immature *P. argus* in temperatures below 23°C.

There apparently is a similarity of percentages of increase per moult between *P. argus* and *P. japonicus* (Nakamura 1940) as shown in Figure 4. The females of this latter species reach sexual maturity between 40 and 45 mm rather like the Bahama population of *P. argus* (misquoted as Florida by Sutcliffe 1952). According to Nakamura, *P. japonicus* reaches this size in about a year and a half. This agrees well with the data for females of *P. longipes* (Table I) in Australia which reach sexual maturity between the first and second year after metamorphosis (Sheard 1949). Although the size of *P. longipes* at maturity is still uncertain, Sheard found some females to be mature between 45 and 50 mm.

It will be noticed that there is no apparent growth of the mature South Shore population (Fig. 2); except for minor fluctuations, the peaks of greatest frequency remain relatively constant between 115 and 120 mm. Further work is required on this question as well as a different approach, although possible explanations are suggested. It may be that growth is slowed down to such an extent by the onset of maturity that individual variations completely obscure year classes. Recent evidence suggests that larger (around 145 mm) lobsters leave or are eliminated from the peripheral areas such as the South Shore and the North Reefs and accumulate in "inshore" situations such as the lagoon and Harrington Sound (Sutcliffe 1953) and in deep water.

SUMMARY

1. Laboratory-maintained specimens of *Panulirus argus* do not increase as much per moult as ones recently brought in from the field. Growth rates obtained from captive lobsters are thus open to question as to their applicability to field conditions.

2. Evidence of the growth rate of *P. argus* in Bermuda is presented in the form of length-frequency graphs com-

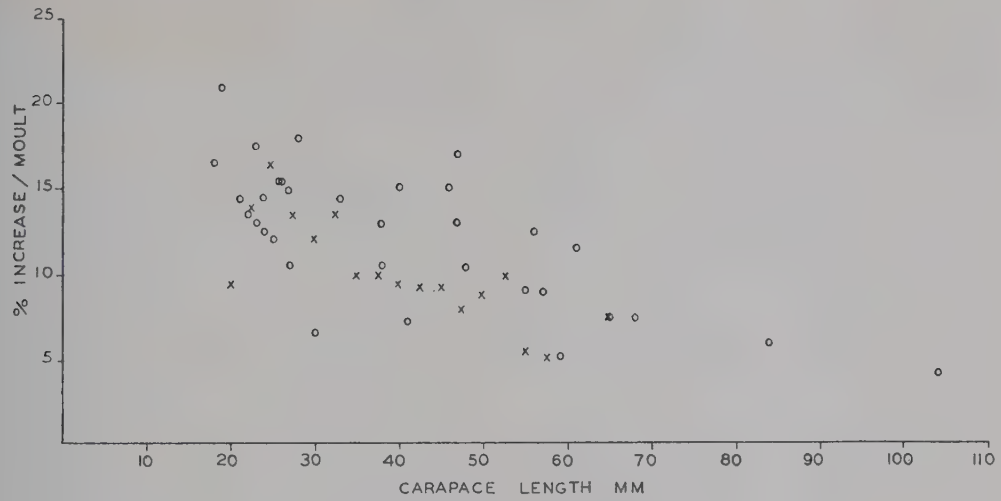

FIG. 4. Comparison of percent increase per moult of recently caught specimens of *Panulirus argus* (o), and *P. japonicus* (from Nakamura 1940) (x). Nakamura's data include 128 specimens.

piled at two month intervals. Although the sample is small (1,435), there is relative clarity of modal progressions throughout a year.

3. An estimate of about three years is given for a spiny lobster to grow from a carapace length of around 6 mm to around 90 mm (sexual maturity) in Bermuda.

4. Data are presented which indicate that the size at sexual maturity of the female may be correlated with temperature.

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A WET-BULB AND DRY-BULB RECORDING THERMOMETER

A continuous record of wet-bulb and dry-bulb temperatures was needed in a study of the effect of temperatures on the nesting distribution of birds. This study was conducted in the Great Smoky Mountains, Tennessee-North Carolina, during one season and in the Chiricahua Mountains, Arizona, in another. The records had to be obtained from rather isolated spots, so the instruments had to operate unattended for several days with their own power supply. The data from a clock-driven recording hygrothermograph of the type commonly used were found to be unsatisfactory, as the temperature and relative humidity elements had different time lags, making it impossible to calculate accurate wet-bulb temperatures. An instrument for directly recording both wet-bulb and dry-bulb temperatures over a one-week period was devised and is described below.

Two Weston metal thermometers measure the temperatures. In this type of thermometer the sensitive bi-metallic element is enclosed in a shaft-like metal shell and the temperature is indicated by a pointer on a circular dial. The sensitive element does not have enough torque to move a pen, so each thermometer was modified by removing the dial and pointer and replacing the pointer by a longer arm with a right-angled point at the indicating end. This arm turns freely. The record is made by periodically (each half hour) striking the indicating points of both thermometers against carbon paper over the recording chart, marking the chart. The length of the indicating arm was chosen with the range of the thermometer (0° to 250°C, in this case, equally 1.6°F per degree of arc) to give the desired range of temperatures on the recording chart, in this case from 40° to 100°F.

The sensitive end of the wet-bulb thermometer is covered with a wick kept wet from a reservoir of distilled water. True wet-bulb temperature is obtained by ventilating this thermometer with a small fan before a record is made; the narrow diameter of the thermometer shaft makes it possible to cool it down to true wet-bulb temperature with little ventilation, less than is required for a mercury-in-glass thermometer of the type usually used in a psychrometer. The fan also ventilates the dry-bulb thermometer; this and the quick response of these thermometers result in a simultaneous record of wet-bulb and dry-bulb temperatures both free of time lag.

The circular chart is driven by a clock with a seven-day rotation and a seven-day wind (Tempscribe clock, Bacharach Industrial Instrument Co., Pittsburgh). This clock also drives the switches controlling the recording circuit.

The general design of the instrument is shown in Figure 1. Mechanical details are not shown because they can be duplicated easily or even improved upon by anybody with fair ingenuity. The recording ends of the thermometer shafts are placed as closely together as possible so that the indicator points travel approximately the same arc. The fan is a 3-to-6-volt direct current miniature motor (Wilson's of Cleveland, Model 6-100) turning a model airplane propeller, and is powered by two No. 6 1½ volt ignition batteries. On the back of the clock is a knob, for setting the clock, which rotates once per hour, and this is used to operate the controlling switches. Because the clock is not designed for operating switches, the switch mechanism must load the clock as lightly as possible. The switches used are snap-action switches designed for coin machines, which operate with very little pressure. The controlling cams, cut from plastic, are shaped so that the instrument completes a cycle and records temperatures every half hour.

Figure 2 is a diagram of the recording circuit. The active part of the cycle begins with Switch A open. Switch C is thrown to terminal 1 by its lever rising on the cam, and the 500 microfarad condenser begins to be charged by a 22½ volt "B" battery through the 100,000 ohm resister, which is in the circuit to prevent high peak currents from otherwise damaging the switch and battery. Switches B and C are operated by the same lever, and simultaneously with the action just described Switch B is closed, which has no effect because Switch A is open. Two or three minutes later the lever of Switch A drops on its cam step, Switch A closes, and the fan motor runs ventilating both thermometers. The condenser continues to be charged. One minute after this the lever of Switches B and C drops on its cam step; Switch B opens, stopping the fan motor, and simultaneously Switch C is thrown to terminal 2, causing the condenser to discharge through the solenoid. The solenoid operates the striker mechanism which strikes the indicator points of the thermometers against the carbon paper and chart. About ten

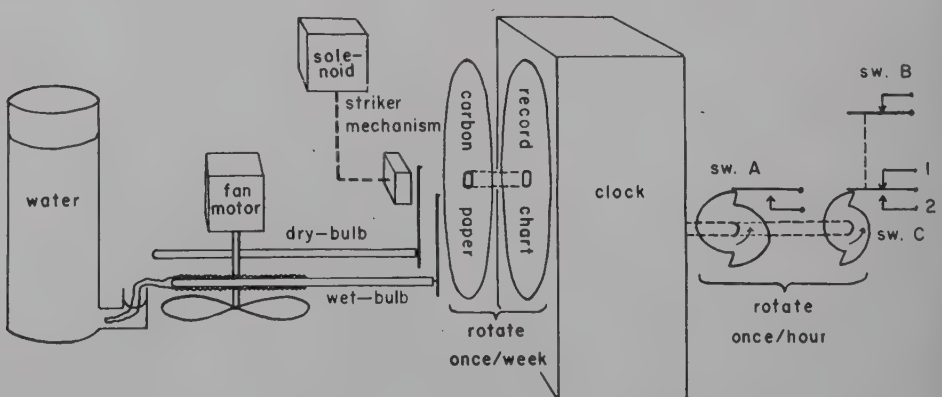

FIG. 1. Schematic diagram of wet-bulb and dry bulb recording thermometer. See Figure 2 for the circuit.

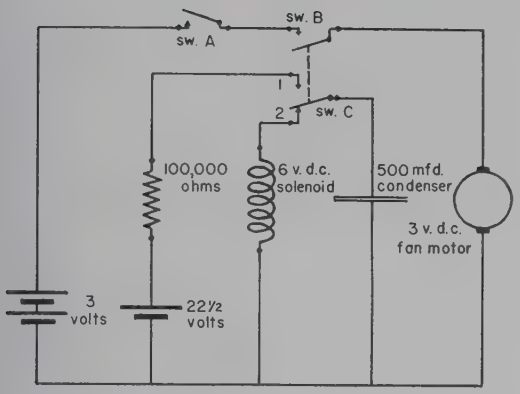

FIG. 2. Circuit diagram of the wet-bulb and dry-bulb recording thermometer.

minutes after the record has been made, Switch A is opened by its lever rising on the cam, resetting that switch for the next cycle. The cycle is repeated very thirty minutes.

The instrument housing encloses the clock, batteries, and controlling and recording mechanisms in a weather-tight box. The sensitive ends of the thermometers are exposed to the outside air but shaded from the sun, and the ventilating fan and water reservoir are also necessarily located outside. In the field each instrument was slung between two trees with a light chain and pulley arrangement so that it could be pulled well above the reach of curious bears and people.

The thermometers were calibrated and a temperature scale constructed for each; the form of the temperature scale and time scale is shown in Figure 3. The temperature record can be read with an accuracy of ±1°F.

Four similar instruments were built. They were used in the field for a two-month period during which they were exposed to relative humidities varying from below 10% to 100% and to rain and fog. They gave very satisfactory performance, the only breakdown being the failure of one motor. During this period the voltage of the 22½ volt battery did not decrease measurably, and the voltage of the batteries used to run the fan motor decreased slightly but not enough to require changing.

The cost of the separate parts for each instrument totalled about $80. The total cost would be considerably

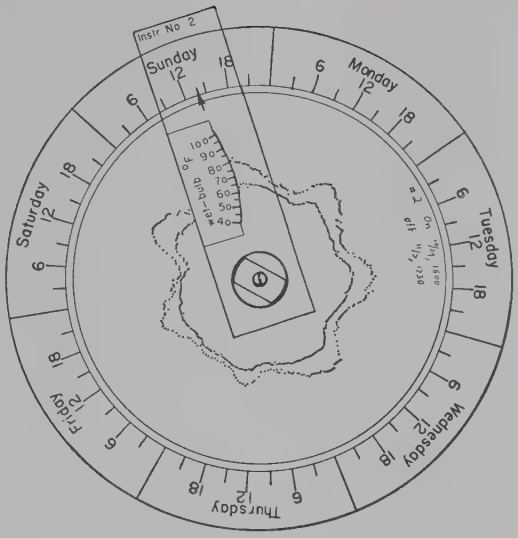

FIG. 3. A week's record of wet-bulb and dry-bulb temperatures, with the time and temperatures scales, about one-half actual size. The inner record is of wet-bulb temperatures. The chart, bearing the records, is positioned correctly on the time scale. The temperature scale is mounted on a transparent arm which is placed over the central hub and can be rotated to read temperature and time of any individual record. A different scale, mounted on a separate arm, is needed for dry-bulb temperatures.

greater if labor were included, because each instrument required much handwork and time in manufacture and calibration. The construction of the original instruments was supported by a Sigma Xi-RESA Grant-in-Aid. The expense of later modifications was borne by the Department of Zoology and Entomology, University, Tennessee I am grateful to Professors J. D. Trimmer and J. W. White of the University of Tennessee Physics Department for several useful suggestions.

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THE ECOSYSTEM APPROACH IN THE TEACHING OF ECOLOGY ILLUSTRATED WITH SAMPLE CLASS DATA

After about 15 years of experimentation in the teaching of ecology, I have come to the conclusion that the ecosystem approach is by far the most effective for a basic "principles" course.* Otherwise the ecology course becomes stymied by, or at least bogged down with, taxonomy. When I first started teaching ecology we talked about environmental factors in lecture and visited various habitats such as lakes, streams, and forests. In the field we collected various organisms and, in the all-too-short time available, made a half-hearted attempt to be quantitative. Back in the laboratory we found that considerable time had to be spent keying down or otherwise associating names with organisms. The net result was that we ended up trying to teach a course in field biology (or systematics) and a course in ecology at the same time without accomplishing anything really worthwhile in

* With general biology, general botany, or general zoology (or any combination thereof) as a prerequisite. It should be emphasied that a principles course in ecology should be on the same level as a basic course in genetics or general physiology, and hence it is immaterial whether it is given in a botany or zoology department (or by coordination of both). The general ecology course is thus designed to provide solid background for plant ecology, limnology, vertebrate ecology, marine ecology, or various applied courses along with such other botany, zoology, and chemistry courses as are needed as prerequisites for the more specialized courses.

either. I am now fully convinced that field biology and ecology cannot be taught at the same time in one quarter or semester. Field biology (field botany, field zoology, general course in systematics, etc.) is an excellent subject in its own right; it would be desirable if all biology majors had such a course or courses especially if they plan advanced work in ecology. However, our experience has shown very clearly that if the ecosystem approach is used a good solid principles course in ecology can be given without systematics of any kind as a prerequisite.

The philosophy of the ecosystem approach is almost exactly the same as that underlying the procedures commonly followed in the general biology laboratory. In general courses we first bring a whole organism of some kind such as the frog, Amoeba, Spirogyra or a flowering plant into the laboratory. After the student has studied the organism as a whole he then dissects (either actually or optically) the specimen and studies the various parts. It is important to note that the reverse procedure would be more or less ridiculous; that is, we would not first bring the student the liver of the frog (or the stamen of the plant) have him study that, then next day bring him the isolated stomach or each individual muscle one by one—and finally during the last week of the course attempt to assemble all the parts into a frog. For one thing we would probably find that there was not enough time to study all the parts. Our poor frog would be most incomplete and probably bear little resemblance to the real frog when we tried to assemble the parts we did study! Yet amazing as it may seem many attempt to teach ecology using this backwards "parts-before-the-whole" procedure (and we confess that we did this 15 years ago!). Actually the "parts-before-the-whole" procedure is even more difficult in ecology than it would be in general biology because the beginning student already has some notion of what the frog or flower is like but generally has very little idea what the whole pond is like. Consequently, it is easy to see why attempting to study details of parts without first introducing the whole is likely to lead to an emphasis on floristics and faunistics rather than on principles of ecology.

Now if we follow our logic one step further it becomes clear that if we are going to introduce the whole system first we should select simplified ecosystems in which the number of important or dominant species is small and the problems of sampling not so difficult as to absorb all the class energy. Otherwise everyone is likely to feel that the data are meaningless because the samples are obviously inadequate. In other words, the first field trip should not be to a large lake or river or a forest because so much of such ecosystems would be physically inaccessible to students and completely unsuited to any reasonable class sampling technics. After several years of experimentation at the University of Georgia we now concentrate on two ecosystems which seem to us ideally suited for class analysis, namely, a small pond and a recently abandoned agricultural field. These ecosystems are not only completely accessible and samplable throughout, but comparison of the two brings out very beautifully many of the most fundamental of ecological principles such as trophic structure, difference between standing crop and productivity, succession, limiting factors and many others.

The difference in objectives of a field biology course and an ecology course can be well illustrated by the choice of study areas. If we were giving a field biology course and simply wanted to collect organisms representing as many taxonomic groups as possible we would visit a small weed-choked unmanaged pond, which would likely contain a large variety of organisms. However, for ecological study a small managed farm-fish pond of about one-half acre is much better because the number of major components is reduced, thereby simplifying identification and sampling problems. For example, essentially all the producer element is in the form of phytoplankton which can be sampled by one metheod; the zooplankton and bottom fauna are of consistent life form, and commonly there are only two species of fish. Absence of complex stratification, etc. (details which would be well covered in a followup course in limnology) make possible satisfactory measurement of major physical factors by students.

Likewise, in selecting an old field for study we have found that a one-year abandoned row-crop field is ideal if the course is given in the fall. Older fields or grasslands can be used but greater taxonomic diversity may increase sampling difficulties. In our area we have not found it difficult to find a suitable study area each year but in some regions it might be feasible for the University to maintain a plot of level land especially for class study part of which was allowed to become fallow each year.

Essentially the same procedures are used in studying the two ecosystems, although the sampling "gear" and the kinds of organisms, of course, are quite different. We divide the class into teams of from one to three students (where the size of class is larger than 15, larger teams could be used) each team being assigned the job of sampling a specific component. Incidentally, we use the word "component" a great deal since it is equally applicable to a taxonomic or trophic unit. Each team works up the data on its particular component and eventually releases them to the whole class. In the pond study the following components are sampled with the equipment used indicated: Phytoplankton (Kemmerer water sampler); zooplankton (plankton net); bottom fauna (Ekman dredge); fish (large seine). Routine physical and chemical measurements are made (field water analysis kit). All samples are taken back to the laboratory where the major organisms are observed in the living condition, and dry weights are determined for all quantitative material. Aliquots of phytoplankton sample are separated both with a Forest centrifuge and a Millipore filter apparatus. Results with these two techniques usually agree reasonably well and provide a good example of the desirability of using more than one method in ecological analysis. For an elementary class it is not necessary to attempt the more difficult separation of particulate nonliving organic matter from the living phytoplankton; the loss on ignition of the filtered or centrifuged material is taken as a rough approximation of phytoplankton biomass (in orther words the living and nonliving combustible material can be considered as belonging to the primary trophic level). However, if desired the chlorophyll method can be used to obtain an estimation of the phytoplankton as such.

In the old-field study each team first "harvests" all the plants in one or more one-square-meter quadrats (usually a total of 10 quadrats are used). The forbs and grasses are carefully pulled up and sorted into paper bags by species; all material from one quadrat is then placed in a large bag. Samples of the animal "standing crops" are then taken as follows: foliage arthropods (standard sweep net with number of strokes sampling 10 m^2 determined from prior research in the specific type of vegeta-

tion); soil arthropods (series of hand sorted quadrats); soil biota (0.1 m^2 soil rings at three depths, extracted in laboratory in a Berlese funnel); small mammals (standard trapline or one-half acre quadrats removal trapping for three nights). Data on average bird populations to be expected are usually provided from research studies, but if there are students in the class especially interested in birds a series of censuses are run during the period of the course. The mammal censuses are also sometimes repeated if there is special interest in them. As in the pond study all material is taken back to the laboratory and dry weights determined (either by actual drying or by use of previously determined wet-to-dry weight conversion factors). Numbers of all above-ground organisms are also recorded so that the interesting relations between numbers and weight can be explored. Soil samples from a profile trench are also taken back to the laboratory, analyzed for sand-salt-clay content by the Bouyoucos method and then sent to the soil testing laboratory for nutrient analysis (or data previously obtained from the specific soil type are made available). Later, temperature and rainfall climographs are constructed from local weather station data.

After the basic data on the two ecosystems have been tabulated the "standing crop structure" of the communities is conveniently summarized by having the students construct biomass pyramids with the components arranged according to trophic levels. Actual data compiled by the 1956 class are shown in Tables I and II and in Figure 1.

TABLE I. Standing crop of major components of a small-pond ecosytem in October 1956

Ecological components	Principal taxonomic components (taxa)	Dry Biomass g/m^2	Dry Biomass lb/acre	Estimated living biomass lb/acre
Phytoplankton (and Tripton)	*Botryococcus* and *Microcystis*	2.79	24.9	250
Zooplankton	*Daphnia*, Copepods, Rotifers	0.31	2.9	29
Benthos	Chironomids, *Chaoborus*	0.73	6.5	58
Fish	*Lepomis macrochirus* *Micropterus salmoides*	3.1	27.6	138

While soil organisms are sampled and studied, as previously indicated, we have found it best to restrict the pyramid of the old field to the above-ground components. Omitting the roots, mycelia and soil animals keep observations within the easy range of beginners, avoids certain troublesome sampling problems, and yet does not materially change the nature of the graphic summary pyramid. As indicated in Tables I and II, weights are expressed both as grams per square meter, the usual ecological unit, and pounds per acre. The latter unit is more comprehensible to the average American student and permits direct comparison with statistics on crop yields or fishery harvests.

From year to year the shape and order of magnitude of the old-field pyramid is similar. At the end of the growing season the old-field has a large standing crop of "producers" and relatively tiny populations of animals. On the other hand, unless a pronounced "bloom" is in progress, the biomass of animals in the pond is usually greater than that of the plant "producers." The shape of the pond pyramid also is much more variable from time to time or year to year. The students are given no suggestions as to possible explanations for these seemingly puzzling pictures but are required to write a paper on

TABLE II. Standing crop of major components of the above-ground portion of an old-field ecosystem at the end of the growing season (late September 1956)*

Ecological components	Principal taxonomic components (taxa)	Dry Biomass g/m^2	Dry Biomass lb/acre	Number individuals (approx.)
Overstory Forb dominants	*Heterotheca latifolia*, *Leptilon canadense*, *Ambrosia artemisiifolia*	360	3208	12/m^2
Understory dominant	*Digitaria sanguinalis*	80	713	75/m^2
Misc. forbs	*Chenopodium*, *Hypericum*, *Cassia*, *Lactuca*, *Gnaphalium*, etc.	29	258	35/m^2
Large insect herbivores (Orthoptera)	*Oecanthus nigricornis*, *Melanoplus femur-rubrum*, *Schistocerca americana*	0.39	3.6	12/m^2
Small insect herbivores	Pentatomidae, Coreidae, Chrysomelidae Miridae, Cicadellidae, etc.	0.21	1.9	146/m^2
Arthropod predators	Araneae, Reduviidae, Coccinellidae	0.004	0.04	4/m^2
Verterbate herbivores	*Peromyscus polionotus*, *Mus musculus*, *Sigmodon hispidus*, fringillid birds	0.06	0.56	16/acre
Vertebrate insectivores and predators	Moles, shrikes, foxes, etc.	**	**	

*Before killing frosts.
**Not determined; biomass very small

these ecosystems in which they work out their own interpretations based on lectures and reading.

Comparison of the pyramids of the two ecosystems not only accomplishes what we discussed at the beginning of the article, namely, providing a picture of the whole, but it brings out very forcefully the difference between standing crop and productivity (probably the most confused concepts in ecology!). It soon becomes apparent to the student that since producer organisms of the old field are annuals then the autumn standing crop is essentially a measure of the *net* productivity. To get gross or total annual productivity we would have to add plant respiration, consumption by animals plus maximum biomass of spring and early summer annuals which have already been returned to organic matter at time of autumn "harvest" (weighing samples of the litter will give an idea of this component). In one-year fields the latter two components are small since the animal crop is very small and the great bulk of the producers are late-summer- or fall-maturing plants. In the pond, on the other hand, the standing crop is in no way a measure of annual primary productivity because the producers have short life cycles and the population may turn over rapidly or be eaten as fast as produced. Fish, however, resemble forbs of the field in that they are longer-lived and grow throughout the season; hence, fish biomass may reflect secondary productivity at that particular trophic level. Thus, important relationships between weight, size and length of life cycles are brought out. In this connection, pyramids of numbers can also be constructed (which will be right-side-up for ponds and up-side-down for fields) but these are likely to be more confusing than useful for clarifying basic principles.

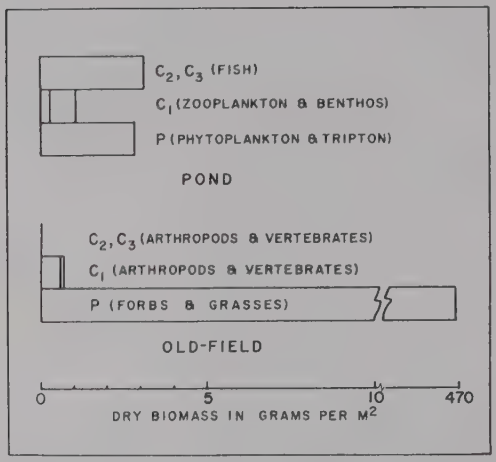

FIG. 1. Biomass pyramids of standing crops present in a small fish pond and a one-year abandoned field during early October at Athens, Georgia. Major components are arranged according to trophic levels as follows: P—producers; C—primary consumers or herbivores; C_2—secondary, tertiary, etc. consumers or predators. Data obtained by the 1956 class in elementary ecology, University of Georgia.

The old-field data are especially suitable for simple statistical treatment since samples are replicated 10 times. Thus, calculation of standard deviations and coefficients of variation for different components emphasize the inherent variability of even a uniform-appearing field. Recognizing and measuring this variability helps the student realize that most ecological differences must be relatively large before they can be considered statistically significant.

Once the gross "structure" of two diverse communities has been roughed out, the class is ready to think in terms of community function or community metabolism. Having discovered that the phytoplankton standing crop gives no clue to primary productivity we return to the pond to set up a "black bottle" experiment designed to demonstrate one possible method of measuring the rate of energy fixation. A series of 6-10 regular B.O.D. bottles are wired to a broomstick and supported about 6 inches below the surface; half of the small bottles are covered with aluminum foil and constitute the "black bottles." Sometimes we also have volunteers run a diurnal oxygen curve (O_2 measurement every two or three hours in a 24-hour period) and we may also run a series of vertical light bottles. It does not matter if these latter measurements are made every year since data obtained in any year are useful in interpreting the results of the annual dark bottle experiments.

A discussion of succession and classification of communities on a functional as well as a structural basis may be profitably undertaken at this point. Thus, early successional communities such as the old field or beginning algal cultures are likely to have a great excess of "plants" over "animals" with the results that production exceeds consumption. The resultant accumulation of organic matter changes conditions, making things favorable for other kinds of organisms. We may then reason that when production balances consumption some sort of stable state or "climax" results. Although usually reserved for more advanced courses it should be pointed out that (1) biomass components may vary widely in metabolic rate and in caloric content and (2) such variations would be considered in more advanced analyses of community function.

The relationship of physical factors to communities and the concept of limiting factors comes next into logical focus. The low values of phosophorus and nitrogen and stimulating effects of fertilizers in both pond water and field soil in the southeast point up the limiting effects of these two nutrients. Comparison of temperature-rainfall climographs with the size of the old-field pyramid base reveals that rainfall is frequently a major limiting factor in productivity, even though the ecologically adapted "weeds" in recent years have proved to be more drought-resistant than some crops such as corn! Simple experimental tests to determine the tolerance of several species of fish to low oxygen tension are also instructive. Thus, the similarities and differences in major limiting factors in terrestrial as compared with aquatic environments are emphasized.

Once the basic picture of the whole has been presented additional studies and discussions can take almost any direction. The instructor can even devote the rest of the time to his own specialty without feeling that he must devote the last few days to synthesis! Specific population components of pond or field can be studied in more detail, laboratory experiments can be set up, or other habitats visited according to local opportunities. We often follow the latter course. The process of ecological succession and competition are brought out by comparison of the plant population of a two- or three-year field with that of the one-year field. Longitudinal succession and a different set of limiting factors and organisms are stressed in a study of a small stream, while stratification and the concept of the climax are illustrated by a visit to a climax forest. As icing on the cake, so to speak, a week-end trip to our Sapelo Marine laboratory always generates enthusiasm. To avoid getting bogged down in too great complexities and thus lose sight of principles we restrict our work to three situations, namely the salt marsh, an estuary, and a sand beach. Special attention to the ecology of oysters and shrimp gives added interest. We have found that the background work on the pond and field ecosystems gives even the elementary student an insight into the complexities of estuarine ecology with the result that our journey becomes something more than a mere collecting trip.

While these extra trips are stimulating and especially feasible in the southeast where the weather is favorable late in the fall (or early in the spring), they are by no means necessary. Various laboratory experiments can be equally effective in bringing out principles. For example, *Chlorella* cultures grown in samples of pond water with and without added nutrients can be used to demonstrate population growth form, limiting factors, productivity and other principles and concepts. Flour beetles or *Drosophila* populations could also be used. Simple field or greenhouse experiments also offer many possibilities.

At the University of Georgia, as in most state universities, many students who take general ecology are majoring in forestry, wildlife management, economic entomology or other fields of applied ecology. The ecosystem approach not only broadens the viewpoint of such students but provides a means of stressing principles which are basic to good management. The technics used

and the difficulties encountered in fish pond management become more intelligible when the whole pond is considered, not just the fish. Likewise the dynamics of small mammal and bird populations reveals principles which are applicable to, but often more difficult to ascertain from, the study of game populations. The role of oxygen in stream pollution, the place of the predator in natural systems, and the problem of the use of insecticides in non-cultivated as compared with cultivated systems are other important practical problems which can be intelligently discussed after the study of pond and field. Since the annual "yield" of woody material in the old field compares favorably with the average annual yield of cordwood from forests we have even discussed the possibility of making paper from "weeds"!

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THE COMPLETE INTERDEPENDENCE OF AN ANT AND A COCCID[1]

Honeydew, the excretion of certain plant-sucking insects, constitutes an essential part of the diet of many species of ants. The ants reciprocate by protecting and often pasturing the insects producing such honeydew.

This reciprocity apparently attains its highest development in the association that exists between the ant *Rhizomyrma fuhrmanni* Forel and a root-feeding coccid closely related to *Eumyrmococcus smithi* Silvestri. (Harold Morrison informs me that a new genus probably will be set up for this coccid and related New World species when they are studied critically.) The ant is an obligate coccidophile, the coccid an obligate myrmecophile.

The ant-coccid association occurs in central Colombia and is known there as the "Hormiga de Amaga." It infests many species of grasses, shrubs, and trees, the most noteworthy being sugar-cane, bananas, coffee, and guava. The infestations of this coccid, however, are limited to a very small proportion of the total number of roots suitable for their sustenance. The principal limiting factors are (1) the confinement of the coccid population to the ant nest, (2) the regulation of the population density of the coccid by the ant, (3) the inherent limitation in the size of the ant colony, and (4) the restriction in numbers of ant colonies imposed by soil conditions and the action of predatory ants.

As pointed out by Roba (1936) the abundance of the coccid and of the attendant ant are directly related. This relation appears to be obligatory and under exact control by the ant. Field observations show that the coccid is limited to the ant nest, can feed only on roots that have been exposed by the ant and is regulated in such feeding by the needs of the ant colony.

The worker *Rhizomyrma fuhrmanni* is obligatorily claustral. Consequently it does little, if any, foraging and there is little if any evidence on the surface of the ground that an ant nest is situated below.

A search for nests of *R. fuhrmanni* is necessarily at random. Since the ant is less than 3 mm in length and the tunnels of the nest vary from 1 to 3 mm in diameter, a cylindrical core of topsoil 8 cm in diameter and 15 cm in length can house a nest complete with workers, males, queens, and brood as well as all stages of the coccid. During this study many such nests were closely examined. The eggs of the coccid and of the ant are stored together in special egg chambers.

A *Rhizomyrma fuhrmanni* colony is stationary and relatively permanent. Presumably it increases in size along the roots of host plants until the maximum population characteristic of the species is attained. Under such conditions the brood may remain static through absorption of the eggs in the ovaries of the queen and the eating by the workers of the deposited eggs.

Since the ant is obligatorily claustral it cannot be forced to leave its nest. Repeated experiments to make it do so have failed. The workers, males and queens in nests artificially opened for free egress remain therein even when such nests are subjected to very high temperatures in complete darkness, to several days' complete submergence in water, and to severance from sustaining host plants.

Presumably each nest of *Rhizomyrma* is originally established by a single mated female. Weber (1944) observed that the nesting flight in another species of this genus occurred on a windless day following a heavy rain. Under such conditions the workers may open the nests and the queens escape, each queen carrying in its mandibles a single coccid. Since the queen in order to excavate her nest must lay aside the stem-mother coccid, the latter is supposedly in an inactive condition. An inactive "resting" or "pupal" stage of this coccid apparently adapted for transportation is commonly found in the egg-chamber of the *R. fuhrmanni* nest.

Since a primary prerequisite for a healthy ant colony is perfect sanitation, the production of excess honeydew must be inhibited. The worker ant apparently accomplishes this by the placement and removal of the coccids on and from the plant roots. The flexibility and the exactness of this regulation is apparent from the fact that in the examination of many nests only 30 per cent or less of the population of adult coccids were on the roots at any one time. That is, about 70 per cent of the total coccid population is continuously held in reserve, "marking time" according to Weber (1944). The coccid was often noted on dead roots, the ant apparently not finding it necessary to remove them. With an abundance of healthy roots available, this reserve of coccids permits an exact regulation of honeydew according to the needs of the ant brood. The amount of honeydew produced may also be influenced by the rate at which the honeydew droplets are removed from the anal extremities of the coccids.

The environmental resistance to the establishment of new nests by the Hormiga de Amaga must be very great. Under natural conditions the action of predators would be expected to cause the greatest mortality, this being done largely through the destruction of the stem-mother queen and her single coccid. That such is the case is indicated by the fact that in old plantations of sugar-cane

[1] This note is based on a study initiated by The Rockefeller Foundation and financed by the National Federation of Colombian Coffee Growers; the study was greatly facilitated by the cooperation of Carlos Carmona B., entomologist, Department of Agricultural Research, Colombian Ministry of Agriculture.

and coffee where cultural practices have permitted excessive erosion of topsoil and the exposure of clay subsoils the colonies of *Rhizomyrma fuhrmanni* are most numerous and those of predatory ants least numerous. Temperature differences between eroded and noneroded soil also may have a marked effect on the ant population. The daily temperature in the nest of the Hormiga de Amaga may be more or less constant at 70°F if a vegetative cover shields the nest from the sun.

The critical factors in determining the number of predatory ants appear to be the nature of the topsoil and the soil cover. The maximum number of such ants apparently occurs when the topsoil is high in humus and well covered with leaf-mulch, such conditions being most suitable for the nesting of these species. With *Rhizomyrma fuhrmanni,* however, the soils apparently most favorable for nesting are high in mineral colloids and low in humus.

The nests of *R. fuhrmanni* are limited to the top 15 cm of soil regardless of soil type. Nests in clay soils are strongly constructed and not readily broken into by soil organisms or by other ants.

Within the limits imposed by edaphic factors and the occurrence of host plants the numbers of coccids appear to be determined by the numbers of *Rhizomyrma fuhrmanni* which in turn are determined by the numbers of predatory ants. The supposed predator species that have been observed associated with the Hormiga de Amaga in central Colombia are species of *Solenopsis, Pheidole,* and *Typhlomyrmex, Leptanilloides biconstricta* Mann, *Rhopalothrix simoni* Em., and *Strumigenys louisianae* Roger. (The identifications of these species were made by M. R. Smith of the U. S. National Museum.)

The nests of Horniga de Amaga are distinctly odoriferous and the coccid appears highly attractive to the workers of *Solenopsis.* Fifty or more adults of this coccid confined in a section of glass tubing that also enclosed a coffee plant root *in situ* were discovered and carried off by this predatory ant.

Since the ant controls the feeding of the coccid it also controls the birth rate of the coccid population. This regulation may be important from the standpoint of susceptibilty of the nest to invasion by predatory ants, the higher the number of coccids per unit of space the greater the attraction to predators.

When edaphic conditions are favorable for the nesting of predatory species of ants, the root-feeding coccid does not become numerous enough to cause noticeable injury to the plants infested. Such edaphic conditions, however, are also favorable for plant growth and the replacement of injured roots.

It is apparent that in Colombia the nesting and nutritive requirements of the *Rhizomyrma fuhrmanni* queen and her brood determines the numerical status of the entire population of its coccid associate, the amount of plant roots for the sustenance of this coccid being virtually unlimited.

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THE KINGDOMS OF THE LIVING WORLD[1]

Division of organisms into the two kingdoms of plants and animals is so familiar, so widely and willingly accepted, that to many biologists it may seem beyond question. Questions there are, however; a number of biologists have proposed three- and four-kingdom conceptions (Haeckel 1866, 1894; Owen 1860, Hogg 1860; Wilson & Cassin 1864; Copeland 1927; Copeland 1938, 1947, 1956; Conard 1939; Rothmaler 1948; Barkley 1949; Cameron 1956) and one (Walton 1930) a single kingdom for the living world, with three subkingdoms. The two-kingdom conception may result largely from the circumstance that the organisms most obvious to man in the world about him are of two major types—higher plants and higher animals. a classification based on fitting all other organisms into two kingdoms suggested by these is likely not to represent the best possible view of the evolutionary and ecological pattern of the living world as a whole.

A recent book by Copeland (1956) expresses the dissatisfaction of some biologists with the two-kingdom system and offers a carefully worked-out classification of the living world into four kingdoms. Copeland considers the most profound distinction among organisms to be that separating those without nuclei from those which possess them. Absence of a distinct and bounded nucleus therefore becomes the defining characteristic of the kingdom *Mychota* (*Monera* in earlier publication), including the bacteria and blue-green algae. A second major group is characterized by the blastula and gastrula stage in development; these are the multicellular animals, kingdom *Animalia.* The kingdom *Plantae* is defined by presence of green chloroplasts, containing chlorophyll and carotinoid pigments and no others; these are the green plants in a narrow sense, excluding most groups of algae. When three kingdoms are thus defined, there remain many organisms which are nucleate, but possess neither blastula and gastrula stages nor plastids, or have plastids with additional pigments; these fall into a fourth kingdom, the *Protoctista.* This fourth kingdom is of admitted heterogeneity, uniting unicellular or acellular with multicellular and multinucleate syncytial forms, grouping together all algae but the green and blue-green, including organisms which seem undoubted plants despite the occurrence of additional pigments, all Protozoa, some of which seem undoubted animals even if their evolution in this direction has proceeded within the limits of a single cell or plasma membrane, and fungi. The kingdom *Protoctista* seems more a product of taxonomic definitions than a grouping of organisms with coherent meaning or common evolutionary theme.

Ecologists are familiar with divisions of the living world which correspond neither to Copeland's nor to the two-kingdom conception. One of these is the fundamental distinction between autotrophs and heterotrophs, by which the bacteria and fungi are separated from their traditional association with the plants, and grouped with the animals. A further division recognizes three major

[1] The author is indebted to Wm. Bridge Cooke for comments on the manuscript.

groups of organisms in the living community: producers, which use solar or chemical energy to synthesize organic compounds from inorganic and provide all the food energy available to the community; consumers, which harvest the productivity of these by eating either producers or other consumers; and reducers, which break down the dead remains of both producers and consumers to soluble or finely particulate form in soil or water, and make available some nutrients for uptake by producers and recirculation through the community. In general, three major modes of nutrition and four major groups of organisms correspond to these three roles in communities. With certain well-known exceptions, the producers may be identified with the green plants and photosynthetic nutrition, the consumers with the animals and nutrition by ingestion. Correlation of the third group, the reducers, transformers, or decomposers, with the fungi and bacteria and with absorptive nutrition is weaker; for absorptive forms include many plants, animals, bacteria, and fungi living as parasites, and animals contribute also to the reduction of dead tissue to the organic matter of soil or water. With its admitted limitations, the three-part view of natural communities seems a useful and meaningful one.

A principal feature of such a conception is that bacteria and fungi are grouped with neither animals nor green plants, but become a third major division. Among the multicellular, or multinucleate forms, the fungi are separated from the true plants as a major group coordinate to both the higher plants and higher animals. Some of the mycologists themselves have advocated such a separation (Martin 1955). Martin (1936, 1940, 1941) regards the fungi as an independent phylum of many divergent series, derived from the flagellates separately from the plants and animals. Fungi are not plants, and their retention in the domain of botany is based on historic association. The terms saprophytic and saprophyte should be replaced, for these forms, by saprobic and saprobe. Rogers (1948) compares evolutionary tendencies of the three groups—plants, animals, and fungi. Tendencies among the plants include photosynthetic nutrition, cutin or cork for control of water loss, extension of the diploid and reduction of the haploid phase. Tendencies among the animals include cytophagy or ingestion, chitin or stratum corneum as protective covering, and early loss of the haploid in favor of the diploid phase. Tendencies in the fungi include absorptive nutrition, escape from the problem of water loss by hidden hyphae, and an extensive dikaryotic phase. The contrasts in these tendencies suggest maintaining the three groups as mutually distinct.

In relation to the central differences in nutrition, the three evolutionary directions may be somewhat differently characterized. The green plants are photosynthetic; correlated with this means of nutrition are a stationary and inactive life, chloroplasts, rigid cellulose cell walls, holdfasts, rhizoids, and root systems for attachment and, often, obtaining nutrients and water, direct exposure of the plant body to sunlight, and evolution of stems and leaves. Animals live by consumption or ingestion, and the active movement which makes it possible; correlated with this is the evolution of the digestive organ system, of the sensory-neuro-motor complex of organ systems for movement and food getting, mostly wall-less cells usually combined with a distinct skeletal system, and a circulatory system for rapid transport of food and oxygen and other functions. Nutrition of the fungi is by absorption; correlated with this are inactive life embedded in the medium or food supply, excretion of digestive enzymes into the medium in many cases, development of hyphae ramifying through the medium, and development also of specialized reproductive structures which, in terrestrial fungi, are the only parts exposed to the air. The most general meaning of these three directions of evolution seems to lie in the three major means of nutrition in natural communities: photosynthesis, ingestion, and absorption. Biochemical, cytological, and other characteristics by which most members of the groups may be distinguished can be recognized; but many, though not all, of these seem correlated with the basic choice of mode of nutrition.

It is suggested that the underlying meaning of the kingdoms of organisms is to be found in these major directions of evolution. Most, though not all, organisms may be grouped around these directions; but only secondarily are the kingdoms taxonomic units for which particular defining characteristics may be chosen. It is in no way inconsistent with such a conception that many of the unicellular forms should not fit easily into any of the three groups, and that forms representing each major direction should have evolved toward the way of life of one of the others—photosynthetic bacteria, absorptive plants and animals, and partly carnivorous plants. Once the three major directions are recognized among multinucleate forms, however, they may be traced into the unicellular forms, and most of these may be assigned to one of the three major directions by their predominant characteristics. A principal difficulty is in the treatment of the bacteria; for a grouping together of bacteria and fungi as a kingdom of saprobes is less convincing on evolutionary grounds than other assignments of unicellular forms.

Any system of kingdoms which is applied as a classification—as distinguished from a recognition of evolutionary directions—to the unicellular forms must encounter difficulties. Copeland's criteria force distribution of the unicellular algae into three kingdoms; and a view of the living world as showing three rather than two major directions of evolution scarcely simplifies the classification of microorganisms. If the kingdoms must be treated as taxonomic units, however, another approach is possible. One may recognize the great matrix of unicellular forms, of many evolutionary lines and diverse nutritive relations, from which the multinucleate forms diverged, as one kingdom, the *Protista*—as suggested by Haeckel (1866), Owen (1860), Hogg (1860), and others. The three major directions among multicellular or multinucleate forms then become the three kingdoms—*Plantae, Animalia,* and *Fungi* (or *Mycetoideum* or *Mycetalia*). It may then be taken for granted that many of the unicellular forms are true plants, or animals, or fungi by any criterion but their unicellular condition, and are as much in the province of the botanist, zoologist, or mycologist, as of the microbiologist.

The living world is, on the protoplasmic level, a single realm; but it is also a realm of immense diversity, of many lines of evolution and more than a million species. It is not to be expected that this realm, which is both one and many, should divide itself neatly into two, three, or four kingdoms. The kingdoms are man's classification, the largest groupings he chooses to recognize by chosen criteria, within the living world. It is suggested that the kingdoms are, most essentially, major directions of evolution. And, if they are so regarded, there is much to be said in favor of a conception based on three directions of evolution—plants, animals, and saprobes—related to three major means of nutrition—photosynthesis, in-

gestion, and absorption—and three major roles in natural communities—as producers, consumers, and reducers.

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A PORTABLE APPARATUS FOR COLLECTING HORIZONTAL PLANKTON SAMPLES[1]

The Chesapeake Biological Laboratory has been conducting a research program designed to provide an adequate method for efficiently and quickly obtaining a sample of oyster larvae representative of the total standing population of a given area, but requiring the counting of a minimum number of samples. The program also includes determining the relationship between such counts of larvae and the resulting set of oyster spat. A practical use that may result is the prediction of the time and relative intensity of oyster sets as indicated by larval abundance in a given area.

The basic equipment described was devised by Manning and Wilcox as an outgrowth of earlier work. It was operated by the author during the summer of 1956 on the St. Mary's River, Maryland, and, on the basis of the results obtained, offers a promising method for measuring larval oyster populations. In the past, sampling on the St. Mary's River has been done from fixed stations and the results indicated that a large number of such samples is needed to show a direct relationship with the subsequent set on test shell bags.

Previous research, particularly that of Manning and Whaley (1954) on the St. Mary's River, has indicated that oyster larvae are usually more abundant in the deeper layers of water than near the surface. It is also known that the distribution and abundance of these populations varies much within a body of water. To obtain a more valid sample, with respect to accurate populations means, horizontal transect samples with a large volume of water should be obtained from the deeper waters.

To accomplish this, use was made of a small gasoline-powered portable pump mounted on a skiff and a pivoted intake pipe that could take samples from the surface to a depth of 12 feet. These running samples were collected at a speed of three to four miles per hour. To retain the larval catch, a number 15 net was mounted on the other side of the boat so that the excess water flowed directly overboard. This size mesh permits most of the straight-hinge larvae to escape but retains all of the umbo stages. These latter are easy to identify and count, and offer a higher degree of correlation with subsequent sets than do samples from fixed stations. A flow meter, designed to deliver eight gallons per minute within ±10 percent accuracy at pressures from 10 to 80 lb/in.^{2}, was used to measure the amount of water delivered to the net. A pressure gage mounted on the outlet pipe indicated pressures from 20 to 40 lb/in.^{2} when in use. Samples of 500 gallons were taken twice a week from the seed area

[1] Contribution No. 109, Chesapeake Biological Laboratory, Maryland Department of Research and Education, Solomons, Maryland. Equipment and facilities of the Laboratory were used. The assistance provided by Joseph H. Manning, G. Francis Beaven, and Merrill Wilcox is gratefully acknowledged.

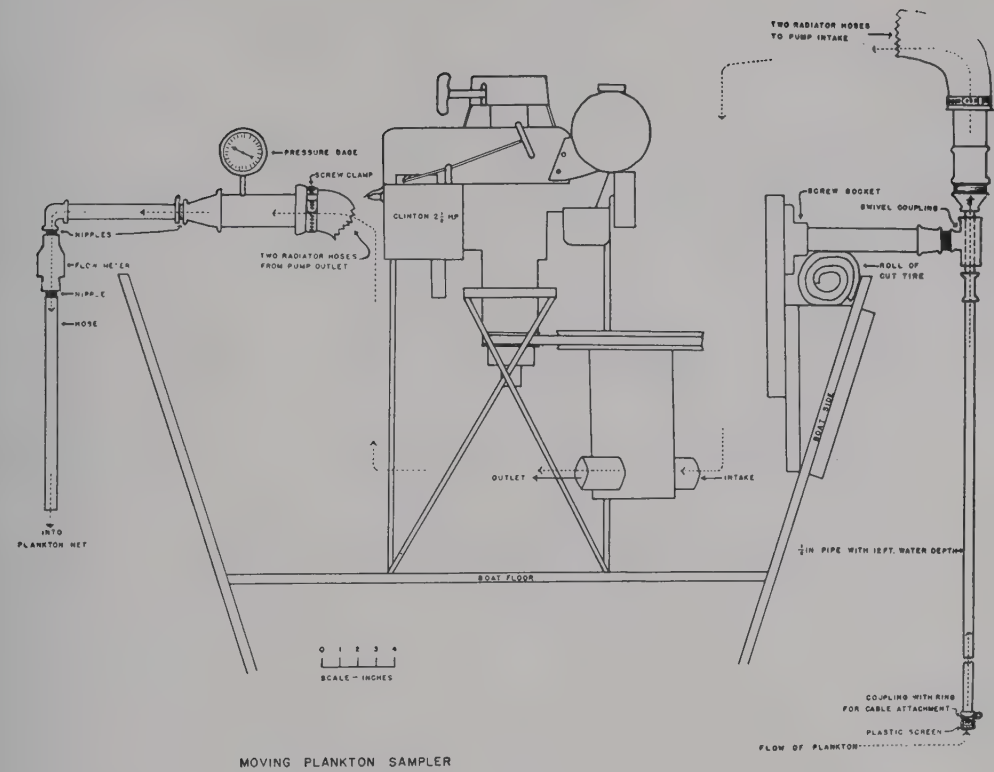

FIG. 1. Portable plankton sampler in cross section of boat.

of the river; actual collecting time for this volume was about an hour and included a distance of three to four miles. It should be pointed out that this pump unit can be adapted not only for collecting representative samples of plankters that swarm, but also for many other kinds of aquatic work.

Each pumping apparatus should be designed to fit a particular skiff and this can then be transferred to other skiffs with minor adjustments. A 14-foot, ½-inch pivot pipe is supported by oak boards mounted to the side of the boat. A rolled strip of airplane tire cushions the vibrations caused by the movement of water past the pipe. Plastic screen is mounted over the free end of the pipe to screen out large organisms and debris. A cable is also attached to this free end to raise and lower the intake to the desired depth; the cable is tied either to the bow or stern of the boat. Car radiator hoses connect the pipe to the pump and screw clamps are used to make the connections tight.

The Haynes Manufacturing Company of Livingston, Texas, mounted a Jabsco Model No. 823 pump to a backpack assembly to operate through a belt drive from a V.S. 400, 2.5 H.P. Clinton engine equipped with centrifugal clutch. This unit is fitted into wooden cross bars on the floor of the boat and also tied to a seat of the boat. Car radiator houses are again used to carry the water away from the pump. The flow meter, manufactured by the Hays Manufacturing Company, Erie, Pennsylvania, is placed at the end of the outlet hose. A nipple at the end of the outlet allows for a rapid change of flow meters if another volume of water or a different time length is desired. A length of garden hose can be attached to a nipple in the flow meter to direct the flow of water into the center of the net. The pressure gage is mounted close to the flow meter and between the flow meter and the pump; this assures the operator that the correct volume of water is being obtained. A net with a 12-inch diameter and cone length of 2½ to three feet was used. These nets may be used four to six times before clogging of the meshes seriously hinders the water flow.

The sample bottle attached to the net held 125 cc of concentrate; this was taken to the laboratory. After killing the organisms with formalin, two soil testing screens with openings of 300μ and 100μ were placed respectively upon one another and the concentrate was thoroughly washed through these. The sample then contained umbo larvae with dimensions of 100 to 300μ. This size-group is believed to have much lower mortality rate than do the straight-hinge larvae and yet there is a time interval before the set occurs that would permit planters to place shells overboard. The larvae were washed from the screen and preserved in 10 cc of two percent formalin. One half of the sample was counted by counting the entire contents of five one-cc samples in a Sedgwick-Rafter chamber using a calibrated binocular microscope. No distortion of organisms occurs with the sampling method described.

The data of our preliminary program indicate a positive relationship between the numbers of larvae and the subsequent set. If the data of our future program continue

to be as promising, we may have a quick and efficient method of predicting the most favorable times for shells to be planted.

Summary

A portable apparatus for collecting horizontal plankton samples and operational technique in using it to collect oyster larvae is described. The unit consists of a small gasoline-powered portable pump mounted on a skiff and a pivoted intake pipe that can take samples to a depth of 12 feet at a speed of three to four miles per hour. This apparatus can be adapted not only for collecting representative plankers that swarm, but also for many other kinds of aquatic work.

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REVIEWS

"Applied Phytosociology"[1]

Angewandte Pflanzensoziologie means applied phytosociology. This is the title of a series of small pamphlet-like publications which has been issuing from the *Bundesanstalt für Vegetationskartierung* (Federal Bureau for Vegetation Mapping) at irregular intervals since 1951.[2] The individual pamphlets vary in size from 29 to 183 pages and each number deals with one topic only; there are two exceptions—one number contains two topics, and another one is devoted to a symposium consisting of 20 papers.

A European phytosociologist is comparable, in the United States, to what Egler calls a vegetationist, or perhaps to a plant ecologist (but very definitely a *syn*ecologist), and very often to a person whose research is focussed on applied synecology. Angewandte Pflanzensoziologie emphasizes therefore the practical aspects of the study of *vegetation,* and the contents of the series faithfully reflect the over-all purpose of the series.

Lest some readers be unfamiliar with the *Bundesanstalt für Vegetationskartierung,* let it be introduced as one of the most important research stations in applied ecology and vegetation mapping of our days. Founded and directed by Reinhold Tüxen, this institute was significant as of its inception, and is today unsurpassed in its field. This success is primarily due to the ability and sustained enthusiasm of its director.

The Angewandte Pflanzensoziologie is entirely in keeping with the high standards of the institute. It is no exaggeration to say that the series is rivalled by few and surpassed by none, and is of fundamental significance for all concerned with research in applied ecology.

Tüxen's adherence to Braun-Blanquet's SIGMA school of phytosociology may result in some hesitance among American readers. But this reluctance is soon dispelled by the quality of the results presented in the Angewandte Pflanzensoziologie. The practical aspects are not only stressed: they are the very *raison d'être* for the entire series, and they are often applicable far beyond the area in which they were established.

An example may serve to illustrate the type of work presented in the Angewandte Pflanzensoziologie.

In No. 6 of the series: *"Auswirkungen der Grundwassersenkung auf die Wiesengesellschaften am Seitenkanal westlich Braunschweig"* Heinz Ellenberg describes the effects of lowering the water table on meadow associations along the Seiten canal west of the city of Braunschweig. The vegetation of the area is carefully mapped just before the water table is lowered artificially, and then again seven years later. Two colored maps at 1:10,000 (6.336 inches per mile) illustrate the effects. As might be expected, a considerable change had taken place in the course of the seven years. A third (black and white) map indicates where the value of the meadows has increased or decreased, in what manner, and to what extent.

The government agency responsible for canal construction had approached the *Bundesanstalt für Vegetationskartierung* with the following four questions:
1. Is it possible to clearly establish the relations between quality and quantity of hay production on meadows (esp. wet meadows) on the one hand, and the depth of the water table on the other, on the basis of the composition of the plant communities, and considering the various conditions of weather, cultivation and fertilization?
2. Is it then possible to establish the increase or decrease in the value of the meadow properties on the basis of the changes in the vegetation and the productivity by weight that result from the lowered water table?
3. What depth of the water table has been found to be the most favorable one in the wet meadows with regard to quality and quantity of hay?
4. Are the usual methods and present experience adequate to answer the above questions, or what further measures should be taken?

In his search for the answers Ellenberg examines: 1. briefly the physical features of the area (topography, geology, climate, soil) and its agricultural characteristics; 2. the water management and its effects on the ground water; 3. in detail, the plant associations; 4. the distribution of the associations before and after lowering the water table; 5. the changes in the floristic composition of the sample areas; 6. the relations of the associations to the depth of the water table; 7. the quantitative productivity of the meadow associations; 8. the quality of the hay; 9. the value of the meadows and its changes, including the justification of demands for indemnity.

Ellenberg then answers the above questions as follows:
1. There is a definite relation between the quantity and quality of the hay production on wet meadows and the depth of the water table, which finds its expression in the floristic composition of the meadow associations.
2. The change in property values can be established adequately on the basis of vegetational changes; this cannot be done on the basis of production by weight because this varies with numerous factors that may be effective for short periods only.
3. The most valuable type of meadow by quality and quantity of hay proved to be characterized by the *Dactylis glomerata-Cirsium oleraceum* association on meadow-moor soils, rich in lime, with a depth of the water table at 75-100 cm in normal years.
4. Present methods and experiences are inadequate to answer questions 1 and 2. But on the basis of this study, Ellenberg is able to conclude his work with a number of proposals and suggestions to close existing gaps.

Of the 13 numbers of the Angewandte Pflanzensoziologie published so far, six include one colored vegetation map each, and one number contains two. All colored vegetation maps are impressive, and color registration and selection are excellent throughout. In addition, numerous well-chosen illustrations, graphs, black-and-white vegetation and other maps are scattered through the

[1] Angewandte Pflanzensoziologie, works from the Bundesanstalt für Vegetationskartierung, Stolzenau/Weser, edited by Reinhold Tüxen.

[2] There are now two journals of the name Angewandte Pflanzensoziologie—the German series reviewed here, and the Austrian series published for the Institut für angewandte Pflanzensoziologie des Landes Kärnten (Carinthia) by Springer-Verlag in Vienna, edited by Erwin Aichinger. Numbers 1 to 11 of the German series are listed in "Books and monographs received for review" in the April, 1957, Ecology. Numbers 1 to 10 of the Austrian series are listed in the July, 1956, issue; and the Festschrift Aichinger of this series was reviewed in the issue of April, 1956. Rev. Ed.

body of the journal; and there are many phytosociological tables to substantiate the texts and the maps. All colored vegetation maps are done on a large scale, ranging from 1:5,000 to 1:25,000. This implies that only a very small area can be covered by any one map. But it is precisely this detail which, according to Tüxen, permits reliable results.

How far this detail can be carried is illustrated on Seibert's map of the forests of Schlitz (ANGEWANDTE PFLANZENSOZIOLOGIE, No. 9), where 134 vegetational units are distinguished on only 28 square miles. Such detail permits a highly differentiated vegetational analysis which, in turn, leads to an accurate correlation between plant communities and site qualities. This correlation is, of course, the most important aspect of the entire vegetation mapping program and gives these maps their great practical value.

In ANGEWANDTE PFLANZENSOZIOLOGIE No. 13, Preising presents his vegetation map of the region around Göttingen; but instead of attaching this map to an elaborating text as is usual, he devises a table on which all major implications are listed for each vegetation unit; this tabular arrangement permits an easy comparison of any association with any other one. The table consists of only six columns but the amount of information on each association and its implications is large and varied.

In column 1, the natural forest associations are given, as well as the plant communities that will take their place under anthropic influences, incl. different kinds of crops, meadow associations, shrub communities, etc. *(Ersatzgesellschaften)*. In column 2, the site is described, covering topography, climate, soils, and soil water characteristics. Column 3 explains the adaptability of these sites to forestry, agriculture, horticulture and settlements (including rural settlements, residential and/or industrial types). In column 4, Preising suggests the most appropriate types of land use, and in columns 5 and 6, he lists trees and shrubs respectively, as the best suited species for hedges, windbreaks, street trees, economic forestry, etc.

Although the title of the institute is Federal Bureau of Vegetation Mapping, the vegetation maps are only a means to an end; a most important means, indeed, but never an end in themselves. The end is always a clearer evaluation of the site qualities, a more rational approach to land use, a greater harmony between natural and cultural forces, a higher yield, a greater stability of the landscape, a more accurate estimate of the productivity (both potential and actual), etc. The vegetation maps and their ecological interpretation are the key to intelligent land use and planning; they are Tüxen's most important product. (Hence his institute is aptly named.)

There has been much criticism of Braun-Blanquet's phytosociological theories, accompanied sometimes by considerable emotional upheavals. Many of the early weaknesses have now been corrected, and the system has been more widely adopted than might have been anticipated at first. The controversy continues, however, and especially in this country few people are enthusiastic about Braun-Blanquet's ideas, and fewer have put them to a test. The ANGEWANDTE PFLANZENSOZIOLOGIE is particularly important from the point of view of testing these theories. They stand or fall with their applicability, and their continued survival depends therefore to a very considerable degree on the validity of the results published in the ANGEWANDTE PFLANZENSOZIOLOGIE.

The critical reader may here remember that the success of Tüxen and his colleagues in applying Braun-Blanquet's theories rests among other reasons on the two facts that an enormous amount of information on the European landscape in general and the vegetation in particular has been amassed in the course of generations, and that the phytosociological theories are sharply focussed on small areas. Much more complex vegetation and dearth of information make it unlikely that these theories can be applied with equal success in many tropical regions, or even in parts of the United States. On the other hand, the ANGEWANDTE PFLANZENSOZIOLOGIE demonstrates that under appropriate circumstances, Braun-Blanquet's ideas can be applied in many fields and to considerable economic advantage.

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GRASSLAND PERSPECTIVE[1]

Ten years have elapsed since "The Grassland of North America" was published. The third printing includes three journal articles which have been published since the original, as well as an introduction to the addenda.

Malin uses the phrase "grassland of North America" in a non-vegetational sense for the area designated as the "trans-Mississippi west." Therefore, ecologists need to be cautioned against inferring the "grassland formation of North America" *(sensu* Clements) in the title. If "Essays on the history of the trans-Mississippi West" were substituted for the present title, however, this stimulating work undoubtedly would have received considerably less attention from ecologists than it deserves.

Malin is an historian, but has an amazing faculty for grasping the essentials of fields seemingly alien to his own, and in doing so he sees things which workers in those fields may overlook. In part one he discusses in six chapters the grass problem, plant ecology, animal ecology, climatology, geology and geography, and soil. In Chapter 7 he presents various ecologists' views of grassland vegetation and ably compares a number of grassland classifications. Chapters 8, 9, and 10 present accounts of early explorations by "forest man" into the "grassland of North America," and factors in grassland equilibrium.

Ecological thinking is not restricted to the first part of the book. In the beginning of part two, in Chapter 11, ecological concepts are discussed. The contributions of such pioneers in grassland regionalism as H. L. Shantz and E. W. Hilgard are discussed in Chapter 12. In the remaining seven chapters essays on agricultural studies, soil physics and tillage, farm organization and others are included.

Malin is conspicuously opposed to the Clementsian mono-climax (climatic) concept. Much of the evidence which he cites to justify his position is of a type which neither destroys nor substantiates Clementsian ideas. In

[1] Malin, James C. 1956. The grassland of North America: Prolegomena to its history. 3rd printing, with addenda. Lawrence, Kans.: J. C. Malin. 469 pp. $4.00.

common with many critics of Clements, Malin fails to separate clearly the theoretical concepts of vegetation from actual vegetation. Since Clementsian classification is on a theoretical or abstract plane (formation, association, etc. are vegetational types, composed in part of theoretical vegetation and in part of abstractions of actual vegetation) it cannot be destroyed by citation of examples of vegetational diversity. The same confusion of theoretical types and actual vegetation appears in the writings of Gleason.

Malin criticizes not only Clementsian terminology but that of others because of "implications of uniformity and rigidity which are so far from reality." In doing so, he fully senses the basis for difficulties in applying any particular vegetational classification. Perhaps Malin is justified in expecting Clements' ideas to fit grassland vegetation because these ideas were developed in that type of vegetation. However, one has only to work in the area to realize that "uniformity and rigidity" within grassland vegetation is a myth, and that grassland vegetation is as difficult to straitjacket as any other.

Malin shows a deep penetration into matters of the actual nature of vegetation when he suggests that we must recognize an east-west gradient of altitude and moisture and a north-south gradient of light period and temperature coupled with analyses of genetic variations within grass species. In this evaluation he displays a grasp of the interplay of genetic and habitat factors within the plant community which many biologists seem not to have. His suggested "nuclear" and "mixed grass" associations follow less logically from his reasoning than perhaps would geographical continuum-types which are oriented east-west and north-south.

The nature of the grassland climax received extensive discussion in the writings of Malin. Since most ecologists are agreed to disagree on the nature of climax, one could hardly expect the matter to be settled in this work. However, Malin cites ample evidence to substantiate his position that the determination of stability in the grassland vegetation is a difficult matter. His proposal that "virgin" is a most inappropriate term for grassland vegetation is followed by a suggestion that "domesticated native grassland" be applied to areas after white man's civilization has affected them and that "native grassland" be restricted to the condition prior to invasion by white man's civilization. The present occurrence of any of the latter type of grassland is certainly open to question; its status alongside *Didus inceptus* seems well established. The term "plowed native grassland" is suggested by Malin for land on which native grass species are growing, but which previously had been plowed or artificially disturbed. One conclusion which emerges from his evaluation is that there is no such thing as an undisturbed grassland.

As an historian Malin is reading the records in detail rather than scanning for "facts" to support a particular botanical theory. It is this historical evaluation which is most illuminating to the ecologist. He quotes from historical records showing that dust storms and prairie fires were regular and accepted features of the area before man moved in with his plow. In fact, many settlers thought that these nuisances would cease as soon as enough of the grasslands were put under the plow. The important point is that, contrary to popular present-day belief, dust storms were prevalent in the grassland areas before settlement occurred. Historical records likewise point out that streams and rivers carried a heavy sediment load before the days of white man's settlement.

As a privately printed work, reproduced from typescript, the text leaves much to be desired in its legibility. Although a regular publishing house might have given it a tidier appearance, as well as the greater publicity which it deserves, the editing usually associated with such publications might well have emasculated the book. Its vigor comes from the challenging suggestions and provoking comments liberally sprinkled throughout the text. As it stands, this group of essays contains the broadest perspective of the vegetational problems of the "grassland of North America" that has been presented. In an area where the vegetational evaluations have been dominated by one ecological school, it is particularly refreshing to have this presentation of different points of view on the nature of grasslands.

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The Living Landscape in Sweden[1]

Sweden can be considered the cradle of modern taxonomy, and it has fostered more than 400 botanists of reputation during the last two centuries. In no other country have the flora and vegetation been studied in greater detail. In spite of the fact that the Swedish people number less than half the population of Canada and less than 1/20 of the population of the United States, they have produced the great Linnaeus, and also Bergius, Forsskål, the many Frieses, the two Agardhs, Kalm, Thunberg, Solander, Wikström, Juel, Lindman, Murbeck, Samuelsson, Kylin, Rosenberg, Sernander, Nilsson-Ehle, to mention but a few of the greatest botanists of the past. Its botany is still dominated by many of the leading men of this field, and nowhere are published as many botanical reports of quality, per capita, as in Sweden at present. All these world-renowned scientists plus the innumerable amateur botanists and botanically interested medical men, clergymen, and other professionals all over the country have contributed very much to the scientific investigation of the region. It is now very newsworthy if a new species is discovered in Sweden or if a plant is found far from its already known area of distribution.

No other country has so many excellent floras and detailed descriptions of the vegetation of most of its regions, from Lappland with its high mountains in the far north to Scania with its beech forests and lovely groves in the far south. Yet, a general description of the vegetation and the flora, or of the living landscape of Sweden, was not written until 1955, when Sten Selander published his large and excellently illustrated book. This was perhaps only natural, since despite the high number of qualified scientists, Sweden has not fostered many great botanists who at the same time were gifted authors. Linnaeus was one of these, as known from his famous travel logs and reports; but few of the later botanists

[1] Selander, Sten. 1955. Det levande landskapet i Sverige. Stockholm: Albert Bonniers Förlag. 485 pp. quarto, with numerous pictures and maps. Sw. kronor 98.00., $19.00.

ever came to his stature in the field of literature. Sten Selander, who at last wrote this scholarly and literate book on the Swedish vegetation, was not only one of the leading plant geographers of the country, a specialist in northern mountains and the discoverer of the most recent and rarest Swedish plants, but also an author of the highest quality. He was One of The Eighteen in the celebrated Swedish Academy, which among other things selects the Nobel Laureates in literature. He died this spring.

This book on the living landscape in Sweden contains 485 pages in quarto, plus numerous pictures of the same high quality as known from the ACTA PHYTOGEOGRAPHICA SUECICA; it is printed on good paper and is a further example of the craftmanship for which Sweden has become so famous.

The introduction states that although the age of machines might be regarded as the end of the Quaternary and the beginning of a new period when Man became a power comparable to the natural forces, the Swedish landscape of Linnaeus was the same as seen by his ancestors nine centuries earlier, but very different from what we see to-day. The known changes are described briefly, their causes discussed, and the almost classical warning against destruction of nature and the disproportionate use of its many resources is repeated with great emphasis before the detailed description begins.

It is not possible to give a complete review of a book which in itself is a compilation of two centuries of researches in a large country. Therefore, a summary of the different chapters must suffice to show how much information has been collected in this single volume.

The first six chapters describe the geological background of the Swedish vegetation and flora. It is pointed out that most of the terrain is formed by the oldest of rocks, and that young formations are found only in the far south. The Pleistocene glaciations have transformed the landscape by aid of ice and water, and alterations in sea level have greatly affected the lowlands and the distribution of the numerous lakes. The groundwater still affects the landscape as does also the climate, which has varied tremendously since the last glaciation ended. There is a distinct biological boundary between northern and southern Sweden, the so-called "biological limit of the Northland," and this phenomenon is explained from the historical and climatic points of view.

After these introductory chapters, Selander describes the different "living landscapes" in greater detail, beginning with the high mountains he knew better than any one else. The different alpine zones are clearly demonstrated by examples of the plants and animals inhabiting them, and their history before, during and after the glaciation is outlined so far as it is known to the botanists. The Swedish tundra, which covers a considerable area in the mountains in the north, is shown to be characterized by the *palsa* formation: tremendous hummocks of uplifted peat with a core of ice, described as "chocolate puddings" three to four or even seven meters high. They occur as far south as central Sweden but are, naturally, most common in the far north. The forests of birch, described next, extend to the tree limit in the north and at high altitudes, and reach also to the lowland in the south, where many of the most delicate flowers are protected by them. Two long chapters discuss the plants of the sea, the coasts, the lakes and rivers, and also the effects of Man's influences on the lakes: pollution, lowering of the surface or drying-out of lakes, damming for power plants, and water-level controls. In the latter chapters numerous observations of international interest are made, and the warnings against unwise changes in lake levels in connection with construction work are perhaps more valid in America than they are in Sweden.

It is but a short jump from the lakes to the different kinds of mires and bogs described in the next chapter, which shows how these formations are affected by differences in geology, soil, and climate. This chapter is concluded by a short description of the history of climates and vegetation which can be read from the mires by aid of palynology, a science invented and developed in Sweden.

Three chapters give accounts of different kinds of forests in the Swedish lowlands (the conifer forest, the groves, and the beech forests), their history is told in great detail as far back as possible, and their future discussed. Descriptions of the heath-landscape and the limited steppes in the south and southeast end the narrative of the wild landscape.

The last chapter reports the influences of cultivation and how Man is changing the living landscape by means of cities, factories, farming practices, and the introduction of exotic plants; the last pages give an account of the future of the living landscape. As long as we have the capital savings of millions of years to waste, Selander points out, it is possible to let economists and engineers decide our course. But as soon as we have to live almost entirely on the annual interest that nature yields, the natural scientists must have the last word. Then the soil scientists must plan the agriculture in detail and the limnologists must take over the management of the water from the engineers who often cannot foresee the consequences of their work. It does not matter then how the natural products are divided, capitalistically or socialistically, since the main point is that there should be enough to divide. A starving world has nothing left for an intellectual society and must certainly fall into barbarism. The only ones who can save the culture are natural scientists: biologists, geneticists, ecologists, soil scientists, since they alone can teach us how to work with, and not against, nature. In a few words: The protection of nature, of living organisms, the water and the soil, is most essential to mankind, perhaps next to the preservation of peace.

The book by Selander on the living landscape in Sweden is too well-written, too filled with wisdom and ecological conclusions of far-reaching importance, in a few words too great a literary masterpiece to be described in a few pages. He ends the introduction with the very true words by Goethe: "So eine Arbeit wird eigentlich nie fertig. Man muss sie für fertig erklären, wenn man nach Zeit das möglichste getan hat." Selander made his book as complete as is possible at present, and no one but he could have written it so superbly.

All ecologists with the slightest knowledge of Scandinavian languages will enjoy reading this book, and even those who do not understand more than the Latin names of the plants will get great pleasure out of the informative pictures taken by many of the most skilled Swedish botanical photographers.

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Scandinavian Ecology[1]

Although ecology in its widest sense is a science followed by many, it has not yet become fully stabilized. Each new prominent worker in the field is inclined to invent a new system, which must be described in a new textbook which in turn will be the basis for the formation of a new school hoped to be better than all the others. This is especially applicable in North America, whereas the older European groups seem to have become a little more stabilized so that some schools now have been tried and modified by some generations of ecologists. This is particularly true for the so-called Uppsala-school, founded by Sernander and continued by Du Rietz and his many qualified students, who have investigated different aspects of vegetation in Sweden during a long period of years. The great number of papers resulting from these studies have been published in Swedish journals and the doctoral dissertations in the famous Acta Phytogeographica Suecica, but a general textbook based on these experiences has not been available although "compendia" by Du Rietz and Sjörs have been used by their students for many years.

This lack of a general textbook based on the hypotheses of the Uppsala-school has now been filled by Hugo Sjörs, who last year published a thorough and concise review of all the phases of these researches. In a concentrated form (229 pages) which sometimes is almost telegraphic in style, he gives very good information about different phases of modern ecology as understood in Scandinavia. He commences by discussing the fields of study in ecology and plant geography, and continues in the next chapter with a review of floristic plant geography: populations, distribution maps and flora manuals, the flora provinces of Scandinavia, floristic elements, disjunct species, endemics and relicts, race formation and ecotypes. Another chapter reviews some autecological phenomena with plant-geographical connections: ecomorphoses, ecomorphological adaptations, amplitudes, pollination ecology, dispersal ecology, effective increase and renewal in the populations. The chapter on synecology gives detailed reviews on ecosystems (in which Sjörs is very critical of the climax hypothesis), plant associations, the characteristics of the site, ecological soil science, and the changes of vegetation and sites in the past and present.

After these introductory chapters on methodology and the basic theories of ecology, Sjörs reviews the vegetation of the sea and the sea-shore, that of the lakes and their shores, and gives a good survey of the different kinds of lakes which are known in such detail from Scandinavian investigations. A chapter on regional distribution of the land vegetation provides a view of major changes in plant cover from the shore to the mountains. Details are then presented in the next five chapters on the vegetation of the heaths in the lowlands, the steppe, the pastures, the mires, and the flora and vegetation of the mountains above the tree limit. The book is concluded by a review of Swedish plant geography, where southern Sweden and northern Sweden are specially described in connection with discussion of the "limit of the Northland." At the end of the book are ten pages of literature cited, a nine-page index of plant names, and the subject index.

As is needed in an ecological textbook of this kind, many good illustrations and maps are met with throughout the text, making it more easily read and understood. The printing is good and there are unusually few direct printing errors. But—and this is a serious but: the book is written in Swedish, and thus is of no use for the teaching of ecology outside Scandinavia. This may be excused by the fact that the book is written for students at Scandinavian universities; but since all of them are required to read foreign languages, it would in no way have hampered their studies if the book had been published in English. It is to be hoped that Hugo Sjörs will soon have occasion to print a new edition of his textbook, preferably in English, so that extra-Scandinavian students will also be able to enjoy his text. This certainly is a more appropriate all-around basic study for prospective ecologists than most other available textbooks the reviewer knows.

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[1] Sjörs, Hugo. 1956. Nordisk växtgeografi. Stockholm, Oslo, Copenhagen, Helsingfors: Scandinavian University Books. 229 pp., 108 figs. Sw. kronor 28.00, $5.50.

Swiss Fir Forests

In the first part of this monograph[1] Kuoch makes a thorough analysis by Braun-Blanquet's plant sociological methods of the Swiss montane forests containing *Abies alba* Mill. Stand surveys totaling 644 are tabulated as documentation for the description, classification, and discussion of ecology, distribution, succession, and silviculture of the 15 plant associations recognized. With the pedologists Bach and Iberg,[2] ecology of the vegetation stands is further defined by means of soil profiles and "differentiating site factors."

Does this study concern American ecologists, when not a single plant association Kuoch describes can be found on the American continent? It does. Kuoch's work was supported by the Swiss Forest Experiment Station and is a fundamental plant sociological study done in most intimate contact with leaders of academic plant sociology inside and outside Switzerland. If not a model for American forestry, Kuoch's thesis should at least cause some re-evaluations of our problem analyses. For none of our forest types do we have such necessary data for management as are provided in Kuoch's work.

More important than Kuoch's sources of support and their implications are the contributions the author makes to plant sociology itself. Kuoch says (p. 134) that, in making a phytosociological study, stands are not selected

[1] Kuoch, R. 1954. Wälder der Schweizer Alpen im Verbreitungsgebeit der Weisstanne. I. (French summary) Mitt. Schweiz. Anstalt für das forstliche Versuchswesen 30: 129-260. 24 tables, 22 figs., photos.

[2] Bach, R., R. Kuoch, and R. Iberg. 1954. Wälder der Schweizer Alpen im Verbreitungsgebeit der Weisstanne. II. Entscheidende Standortsfaktoren und Böden. (French summary) Mitt. Schweiz. Anstalt für das forstliche Versuchswesen 30: 261-314. 1 table, 5 figs.

Parasite Ecology[1]

In Parasites and Parasitism Thomas W. M. Cameron has written an excellent survey of the phenomena of animal parasitism, particularly interesting because he has always kept in mind evolutionary phenomena and relationships. In writing about parasitism he is, of course, writing about ecology. This is explicit in the first sentence of the book, which in a way sets the theme: "No organism is an entity unto itself; it lives as a member of a community and the life processes both of itself and of its neighbors act and interact on each other."

Mr. Cameron wisely avoids attempting any rigid definition of parasite or parasitism, remarking only that "the words are used in the wide general sense as referring to an organism which is dependent for some essential metabolic factor on another organism which is always larger than itself." His discussion, however, is limited to cases in which the host is an animal, thus avoiding parasitic relations of plants with plants or of animals with plants.

The first two-thirds of the book are devoted to a systematic survey of "The Parasites" which are grouped broadly into Protista (bacteria, fungi, spirochaeta, protozoa, viruses and rickettsiae), Lower Metazoa and Higher Metazoa. Parasites of man and domestic animals inevitably get a great deal of attention because they are best known, but the emphasis is not on medical or veterinary problems as such, but on kinds of parasitic relationships, including nonpathogenic relationships. Mr. Cameron has managed to summarize an enormous amount of biological information. Even such well-worn parasites as the plasmodia of malaria and the trypanosomes of sleeping-sickness get a fresh perspective with this treatment. There are numerous illustrations of different types of parasites and a particularly fine series of diagrams of life cycles.

The last part of the book is called "The Host and Its Reactions." The several chapters of this section are remarkable because of the skill with which the author has blended concepts from immunology, epidemiology and ecology to develop his particular discussions, which continue to turn largely on evolutionary questions.

The book was written as a textbook and I should think it would be splendid for this purpose, providing a rich factual basis around which a variety of interesting lectures could be developed. It is also a compact reference survey of the parasites of animals, but for this purpose I wish the author had documented his sources through the text. There is a well-selected bibliography at the end of the book, but no indication of sources in the text itself.

The section on "The Host and Its Reactions" should provide thought-provoking reading for every ecologist. There is no explicit attempt to develop ecological principles as such, but the whole section is written from a point of view that can most aptly be called "ecological."

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[1] Cameron, T. W. M. 1956. Parasites and parasitism. New York: John Wiley & Sons; London: Methuen & Co. Ltd. xix + 322 pp., 115 figs. $6.75.

The Natural History of Snakes Inhabiting the United States[1]

Books dealing with reptiles, including check lists, generic monographs, faunal studies of counties, states or regions, as well as general accounts have been pouring off the presses at an unprecedented rate during the last decade. But not since 1941, when the very useful Field book of snakes of the United States and Canada by K. P. Schmidt and D. D. Davis appeared, has anyone attempted to cover the entire ophidian fauna of the United States. With 114 species to be dealt with this is something of a task, a task made no easier by the inclusion of subspecies, many of which have been erected on the basis of studies far too incomplete to be called scientific.

Thus in this new handbook prepared by the Wrights of Cornell, they have felt impelled to consider a total of 305 subspecies, including problematical forms listed by subspecific names but often discussed as "variants." These questionable forms are mostly from the eastern portion of the United States. The snakes of the western states are much more adequately understood, largely because of the meticulous work of L. M. Klauber, whose monographs of genera with species represented in the Southwest have set standards that ought to be more widely emulated.

Like many of the better handbooks, this one dealing with the snakes includes much more than keys, descriptions, distributional maps, and illustrations. In addition to such data, the accounts of each subspecies and "variant form" incorporate information concerning habits and habitat, periods of activity, reproduction, ecdysis, feeding habits, enemies, and longevity when such data are available. Miscellaneous information is included under field notes, with authorities cited for varied and sundry facts or speculations that the Wrights find interesting or believe to be important. Some space has been devoted to the venoms of the rear-fanged species as well as to those potentially dangerous to man—19 of the 114 species discussed.

An introductory chapter discusses common and scientific names (with a tabulation of the number of genera and "forms" in each of the five families represented, but curiously with the numbers of species omitted) and the problems of classification, and provides a sort of summary of the data incorporated under various topics in the individual accounts in the main body of the text. Here also are half a dozen maps of the United States. Two of them show the distributions of some of the more important species of plants, using data principally from Clements and Shelford, Livingston and Shreve, and Sargent. The third, without recourse to color, attempts to show geological structures and formations. The fourth depicts biotic provinces in terms of the distributions of forests and trees. The fifth, which seems to have more bearing on the distributions of reptiles than the others, shows the physical divisions. Finally there is a map of

[1] Wright, Albert Hazen & Anna Allen Wright. 1957. Handbook of snakes of the United States and Canada. Ithaca, New York: Comstock Publishing Associates (Cornell Univ. Press.) 2 vols.: vol. 1, pp. i-xviii, 1-564, 167 figs., 43 maps; vol. 2, pp. i-ix, 565-1106, 239 figs., 37 maps. $14.75.

"plant growth regions," with normal mean isotherms added for good measure. The bearing these maps have on the distributions of snakes is not discussed, but perhaps their inclusion will make evident the complexity of environmental factors restricting the dispersal of snakes. It is noteworthy that of 114 species in the United States, only 22 have distributions extending into Canada.

The inclusion of maps showing the ranges of virtually all subspecies, many of which have not previously been mapped, is a notable contribution. Some extralimital records, such as that for the Sonoran coral snake in Idaho, certainly should have been questioned, whereas other maps reflect little more than the dubious and unsatisfactory state of our knowledge. These, perhaps even more than the questions the Wrights often raise, will serve as a stimulus to those looking for problems to solve. Indeed the Wrights have further paved the way by their citations of sources for additional information. A comprehensive bibliography containing titles in full will appear in a third volume still to come. Only those references the Wrights consider important are now listed. There is a glossary as well as an index to the names of authors and to species or subspecies mentioned in the text.

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NATURAL HISTORY OF BIRDS[1]

This book is intended as a general reference to the classification, anatomy, physiology, behavior, ecology, and economic relations of birds. The objective of the author is to explain the *why* as well as the *what* and the *how* of bird life and its problems. A large amount of subject material is touched upon and there is a selected list of references that includes about 500 titles. Three chapters of special ecological interest deal with Bird Distribution, Ecological Relations of Birds, and Bird Abundance.

The chapter on Bird Distribution may be taken to illustrate the manner of treatment. In the introductory paragraphs, distribution is said to be affected by factors either *ecological,* concerned with the suitability and development of the habitat, or *historical,* involving the evolution of birds to fit the habitat and the general development of land and its attributes, but the factors involved are not listed. ". . . the prime element that . . . controls their distribution is a suitable climate . . . the most important influence of climate on birds seems to be this indirect one through cover." There is no discussion of the direct effects of climatic factors in controlling distribution, although barriers are classified into *zonal* (temperature, daylight), *humal* (atmospheric humidity), and *associational* (territory, food, breeding places, cover, special needs). The principle of *limits of tolerance* is mentioned, but not explained, elsewhere in the book in connection, strangely enough, with structural adaptations.

In a section entitled "Zoogeographic Laws," reference is to the classical statement that "all animals are found wherever conditions are suitable unless (1) they are unable to reach an area, (2) they reached an area but were unable to survive, or (3) they reached an area and evolved into another species." These ideas are adequately explained and illustrated.

Under "Pathways of Spread," the Alaskan and Panamanian land bridges are referred to and later in the chapter Mayr's (1946) treatment of the origin of North American birds is reviewed.

Zoogeographic realms, life zones, biomes, and biotic provinces are briefly referred to but not sufficiently described or characterized to be much use to the student. For instance in regard to biomes, about all that is said is: "The principal characteristics of the biome system are a series of large regions based upon the major features of plant distribution, which in the Holarctic world give Tundra, Coniferous Forest, Deciduous Forest, and Grassland biomes. These are climax areas—meaning permanent areas determined by climate." Considerable emphasis, however, is placed on the importance of vegetation in controlling bird distribution. The niche segregation of four species of grouse in Wisconsin in the ecotone between prairie and forest is diagramed to illustrate succession.

The common ecological rules of Bergmann, Allen, Gloger, and others are given. A table of bird weights to illustrate Bergmann's rule is presented for 19 species both for a "cooler region" and a "warmer region." There is no indication where these weights were obtained, number of records on which they were based, or their statistical reliability.

There is discussion concerning the change in habits of some species with advent of man. There are remarks concerning the size of ranges, continuous and discontinuous ranges, mobility of birds, difference between allopatric and sympatric species.

Other chapters follow in similar vein. One comes frequently on statements that are difficult to understand: (page 179) "The governing point in bird distribution seems to be the actual condition of the habitat—*the life form*—not the major feature of the landscape." (page 209) "A bird that lives in the woods . . . does so because woods alone supply its instinctive needs for habitat." In the chapter on Bird Abundance, the statement is made (page 250): "Limiting factors are the nine intertwined ecological constituents of *productivity* . . . ." (page 263) ". . . because the climax appears to be the most efficient energy stage, it seems likely that it in turn supports a higher population of birds . . . sometimes more than 25 per cent greater." (page 265) There are occasional statements that are downright inaccurate (page 109): "The incubation temperature approaches that of the incubating bird, which ranges from about 100°F. to 110°F. in different species. (It has been reported that the most rapid development occurs at a temperature several degrees above the body temperature for the species.)" There is no mention of Huggins' study (ECOLOGY 22: 148-157, 1946), in which the egg temperature in wild birds during incubation was found to average only about 93°F.

Throughout the book there is frequent mention of pertinent concepts without attempt at defining or explaining what they mean or their significance to the matter under discussion. This, for instance, occurs in respect to density-dependent and density-independent factors on page 251 and on the next page, competition, cooperation, and

[1] Wing, Leonard W. 1956. Natural history of birds. A guide to ornithology. New York: Ronald Press. xi + 539 pp., 221 figs., tables, 4 appendices. $6.75.

disoperation. Nor are any of these five terms listed as such in the Glossary, although under "Density Relations" is found, "Conditions governed by the number of birds are called "density dependent"; those not so related are called "density independent."

Some topics are presented in an uncritical manner. One page 253 there is a short favorable discussion of *extinction threshold* and Darling's (1938) principle. There is no reference to the important studies of Smith (Ecology 24: 183-207, 1943), Richdale ("A study of a group of penguins of known age," 1949), and others that cast considerable doubt on the validity of this principle.

There is no need to multiply instances of criticism of this sort. The book on the whole is admirably conceived in trying to cover the whole field. It is suggestive of many things and some parts of it show imagination in presentation (such as the illustration on the function of the cranial nerves, page 74). Unfortunately, however, the book cannot be considered authoritative or a dependable reference.

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